UNIVERSITÉ LAVAL

ANALYSE SPATIALE, SÉLECTION DES PAYSAGES ET STRATÉGIES DE CONSERVATION EN PRÉSENCE DE RÉGIMES MULTIPLES DE PERTURBATION: LE CAS DU CARIBOU FORESTIER EN FORET BORÉALE AMÉNAGÉE

Thèse

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RÉSUMÉ

Identifier les processus écologiques (a)biotiques qui sous-tendent les patrons de distribution d'espèces et de dynamique de population est fondamental pour conserver efficacement les espèces menacées d'extinction. Cette thèse poursuit un double objectif: 1) comprendre les processus écologiques qui régissent la sélection des paysages du caribou forestier (*Rangifer tarandus caribou*) et 2) évaluer l'efficacité des politiques actuelles d'aménagement du territoire pour cet écotype. Le premier chapitre s'inscrit directement dans le premier objectif en présentant une nouvelle méthode numérique d'inférence statistique capable de modéliser l'autocorrélation spatiale présente dans les données de distribution d'espèces. Cette méthode utilise *integrated nested Laplace approximations* (INLA) au lieu des simulations *Markov chain Monte Carlo.* Je montre, qu'en plus de produire des résultats exacts et rapides, l'utilisation d'INLA permet de modéliser l'autocorrélation spatiale résiduelle tout en estimant adéquatement l'incertitude des paramètres et des prédictions du modèle. Dans le deuxième chapitre, la methode INLA est utilisée pour tester lequel des processus, parmi le climat et la distance aux routes, explique les gradients géographiques dans la sélection des paysages par le caribou forestier. Les résultats montrent une prépondérance de l'effet des routes par rapport au climat. De plus, les parterres de coupe étaient deux fois plus évités que les brulis récents. Ces résultats appuient une gestion de l'habitat du caribou forestier qui limite l'étalement du réseau routier et qui distingue l'effet des coupes forestières de celui des feux. Le dernier chapitre explore grâce à un modèle de simulation des paysages spatialement explicite les interactions spatiales entre un réseau d'aires protégées, la récolte forestière et les feux afin de quantifier leurs effets sur la dynamique de population du caribou forestier et sur les coûts économiques liés à l'aménagement forestier. Je montre la nécessité d'inclure les contarintes liées aux feux et aux aires protégées dans le calcul des niveaux de récolte, sans quoi ces niveaux ne sont durables ni pour le caribou forestier, ni pour l'industrie forestière. Les feux augmentent l'antagonisme existant entre exploitation forestière et conservation, avec ou sans coupes de récupération après feu. Cette étude illustre donc la nécessité de mieux comprendre les interactions spatiales entre dynamique des populations, aires protégées, aménagement forestier et régime de feux pour développer des stratégies de conservation qui soient plus efficaces.

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ABSTRACT

Linking spatial patterns of species distribution and population dynamics with biotic and abiotic processes is central to inform effective conservation planning for endangered species. This thesis investigated how linking spatial patterns of boreal woodland caribou (*Rangifer tarandus caribou*), hereafter boreal caribou, to processes can 1) improve our understanding of landscape selection of this ecotype and 2) inform the efficiency of current land use policies in practice. I first present a new powerful numerical method that allows integrating properly spatial information present in species distribution data to make accurate statistical inference. This method uses integrated nested Laplace approximations (INLA) as an alternative to Markov chain Monte Carlo simulations. I show that, in addition of being accurate and rapid, the use of INLA with Bayesian hierarchical spatial models efficiently accounted for spatial autocorrelation in the residuals and fairly evaluated uncertainty in parameter estimates and predictions. I then used INLA to test which ecological processes, among climate and the distance to roads, drove the existence of geographical patterns in boreal caribou landscape selection. Data supported road-driven selection over a climate influence. Moreover, I show that boreal caribou avoidance of logged areas was two-fold stronger than burned areas. Together these results indicated that limiting the spread of road networks and accounting for the uneven impact of logging compared to wildfire should be integral parts of any habitat management plan and conservation measures within the range of this ecotype. Finally, I use a spatially explicit landscape simulation model to explore how spatial interactions among protected area networks, industrial forestry and fire regimes impacted the population dynamics of boreal caribou and the economic costs related to forest management. I show that the current policy of conservation planning and forest management in the Côte-Nord region in Québec is unlikely to be sustainable for either boreal caribou conservation or timber supply mainly because of current overestimated planned harvest levels. Fire increased antagonisms between current practices of forest management and habitat conservation, irrespective of the presence of salvage logging. This study illustrates that efficient conservation planning requires a better understanding of spatial interactions among population dynamics, protected area networks, forest management, and fire regimes.

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AVANT-PROPOS

Ma thèse comprend trois chapitres écrits en anglais sous forme d'articles scientifiques pour publication. Pour chaque chapitre, je suis l'auteur principal et ai réalisé seul ou en collaboration les étapes suivantes: 1) la conception de l'étude et la définition des objectifs; 2) la préparation, la vérification et l'analyse des jeux de données, ainsi que pour le troisième chapitre, l'élaboration et la construction du modèle de simulation dans SELES; 3) l'interprétation et la discussion des résultats; et 4) l'écriture des manuscrits et la réalisation des figures, tableaux et annexes des trois chapitres.

Le premier chapitre décrit une nouvelle procédure statistique pour calibrer des modèles hiérarchiques bayésiens spatiaux. Il a été écrit en collaboration avec Sara Martino, Håvard Rue et Steven G. Cumming et a été publié en 2012 dans la revue *Methods in Ecology and Evolution* sous le titre « *Hierarchical analysis of spatially autocorrelated ecological data using integrated nested Laplace approximation* ». Sara Martino et Håvard Rue sont respectivement stagiaire postdoctorale et professeur à la *Norvegian University of Science and Technology* et Steven G. Cumming est professeur au département des sciences du bois et de la forêt de l'Université Laval. Le deuxième chapitre vise à identifier les raisons biologiques qui sous-tendent l'existence de gradients géographiques dans la sélection des paysages par le caribou forestier. Ce chapitre a été écrit en collaboration avec Eliot J.B. McIntire, chercheur scientifique au Centre de Foresterie du Pacifique à Victoria, Daniel Fortin, professeur au département de biologie de l'Université Laval, Steven G. Cumming, Frédéric Raulier, professeur au département des sciences du bois et de la forêt de l'Université Laval, Pierre Racine, professionnel de recherche au Centre d'Étude de la Forêt (CEF) et Claude Dussault, biologiste à la Direction de l'expertise du Ministère des Ressources naturelles et de la faune du Québec. Ce chapitre a été publié en 2013 dans la revue *PLoS ONE* sous le titre « Explaining geographic gradients in winter selection of landscapes by boreal caribou with implications under global changes in eastern Canada ». Le troisième chapitre vise à évaluer les compromis possibles entre aménagement forestier et conservation du caribou forestier sur la Côte-Nord. Ce chapitre a été réalisé en collaboration avec Eliot J.B. McIntire et Frédéric Raulier et sera soumis pour publication très prochainement.

INTRODUCTION GÉNÉRALE

Mise en contexte

L'étendue actuelle des changements environnementaux à l'échelle mondiale qui sont attribuables aux changements climatiques et à l'altération humaine des paysages menace de nombreuses espèces dont les capacités adaptatives (e.g. tolérance écologique, potentiel de dispersion) sont insuffisantes pour s'adapter à la rapidité de tels changements (Thuiller 2007, Barnosky *et al.* 2011). Dans ce contexte, il est urgent de 1) quantifier et comprendre les impacts causés par les changements climatiques et la dégradation humaine des paysages, sur la distribution spatiale des espèces vulnérables et menacées d'extinction; et 2) d'évaluer l'efficacité écologique et socio-économique des stratégies de conservation visant à réduire les impacts négatifs de ces mêmes perturbations environnementales.

Le caribou forestier est l'un des trois écotypes, avec l'écotype migrateur et montagnard, qui appartient à la sous-espèce caribou des bois (*Rangifer tarandus caribou*). Le caribou forestier a le statut légal d'espèce menacée au Canada selon la Loi sur les espèces en péril (L.C. 2002, ch. 29) et le statut d'espèce vulnérable au Québec selon la Loi sur les espèces menacées ou vulnérables (L.R.Q, c E-12.01). Autrefois présent partout au Canada et dans le nord des États-Unis, la limite sud de son aire de répartition géographique au Québec n'a cessé de régresser vers le nord depuis le milieu du XIXe siècle (Courtois et al. 2003). Au Québec, des inventaires aériens ont permis de constater le déclin et l'état précaire de plusieurs hardes (Équipe de rétablissement du caribou forestier du Québec 2013) ce qui, jumelé à une contraction de son aire de répartition, a d'importantes conséquences écologiques, sociales et culturelles, notamment pour plusieurs Premières Nations dont les modes de vie sont étroitement liés à l'abondance du caribou.

La principale hypothèse pour expliquer le déclin des populations de caribou forestier est l'accroissement des taux de prédation qui résulte de la perte, de la dégradation et de la fragmentation de son habitat naturel causé directement par les activités humaines, comme celles liées aux opérations de récolte en matières ligneuses (Festa-Bianchet et al. 2011;

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Environnement Canada 2012). L'altération anthropique de l'habitat naturel du caribou favorise des densités élevées de proies alternatives telles que l'orignal (*Alces alces*) et le cerf de virginie (*Odocoileus virginianus*), ce qui induit une augmentation des populations de prédateurs comme le loup gris (*Canis lupus*) et l'ours noir (*Ursus americanus*) et, par effet ricochet, accroît le risque de prédation sur le caribou forestier (Environnement Canada 2012). Les impacts négatifs des activités anthropiques, notamment des coupes forestières et des routes, sur la dynamique de population de nombreuses hardes de caribou des bois supportent cette hypothèse (Courtois *et al.* 2007; Sorensen *et al.* 2010; Wittmer et al. 2007; Environnement Canada 2012).

Toutefois, contrairement à l'écotype migrateur (Sharma et al. 2009), il existe peu d'informations quantitatives à propos du rôle que pourrait jouer le climat sur la sélection des paysages et la distribution du caribou forestier à grande échelle spatiale. Le climat peut influencer le caribou de multiples manières, notamment en modifiant le régime des feux (Boulanger et al. 2013), l'accessibilité et l'abondance de la nourriture ou encore en augmentant le niveau de harcèlement causé par les insectes (Vors et Boyce 2009). Dans les paysages forestiers où l'empreinte des activités humaines est encore relativement modérée, comme on en rencontre dans la partie nord de la forêt commerciale de la pessière noire à mousses au Québec, il est possible que la variation spatiale du climat joue un rôle plus important sur sa distribution spatiale à l'échelle régionale que dans les paysages fortement altérés par les activités humaines (ex : Alberta, Colombie-Britannique). Il est également possible que les gradients géographiques observés dans la sélection des paysages par le caribou forestier au Québec (Fortin et al. 2008) trouvent leur origine dans la variation spatiale du climat (hypothèse 1) ou dans la distance par rapport aux activités humaines (hypothèse 2), voire d'une interaction entre ces deux alternatives (hypothèse 3).

Par ailleurs, outre l'effet possible du climat, on ignore si l'effet des feux est équivalent à celui des coupes sur la sélection des paysages par le caribou forestier au Québec. Ce point est pourtant important dans le cadre de l'aménagement forestier écosystémique dont une des prémices est de substituer le taux de perturbations naturelles par des coupes de même intensité, superficie et de configuration spatiale.

Tester ces hypothèses, rejoint un enjeu central en écologie des paysages et en conservation, qui consiste à identifier et quantifier les processus écologiques qui influencent la distribution spatiale des espèces à statut précaire. La réalisation de cet objectif soulève cependant des questions méthodologiques importantes, notamment en ce qui concerne la modélisation de l'autocorrélation spatiale, un phénomène qui est présent dans un grand nombre de jeu de données sur la distribution spatiale des espèces et qui peut accroître l'erreur de type-I durant les analyses et ainsi invalider les inférences statistiques, s'il n'est pas pris en compte (Legendre 1993). Les deux premiers chapitres de cette thèse adressent donc spécifiquement ces enjeux, à savoir 1) développer des outils statistiques robustes et non-biaisés pour analyser des données de distribution d'espèces spatialement auto-corrélées (chapitre 1); 2) identifier quel processus écologique, parmi le climat et la distance par rapport aux routes, explique les gradients géographiques dans la sélection des paysages en hiver par caribou forestier au Québec (chapitre 2) et 3) tester si l'effet des coupes est équivalent à celui des feux sur la distribution spatiale du caribou forestier (chapitre 2).

Par ailleurs, le statut légal d'espèce vulnérable du caribou forestier a mené le gouvernement du Québec à établir une stratégie de rétablissement visant à enrayer le déclin des populations (Équipe de rétablissement du caribou forestier du Québec 2008, 2013), notamment dans la zone d'exploitation forestière située à l'intérieure du domaine bioclimatique de la pessière noire à mousses. L'efficacité à moyen et à long terme de cette stratégie de conservation mise en place sur le terrain n'est toutefois que très peu documentée en termes de probabilité de persistance des populations de caribou (indicateur écologique) et de viabilité économique des activités d'aménagement forestier (indicateur socioéconomique). Évaluer la réponse de ces deux indicateurs simultanément est pourtant indispensable pour juger du niveau d'efficacité de toute mesure ou stratégie de conservation (Naidoo et al. 2006). Le troisième et dernier chapitre de cette thèse vise à améliorer nos connaissances dans ce domaine et à adresser spécifiquement cet enjeu à l'aide d'une étude de cas dans la région de la Côte-Nord, située dans l'est du Québec.

Autocorrélation spatiale et modélisation de la distribution spatiale des espèces

L'amélioration de nos connaissances sur les relations entre la distribution spatiale des espèces et leur environnement, notamment leur habitat, ainsi que le rôle joué par les perturbations environnementales, repose en partie sur la disponibilité des données et des méthodes quantitatives adéquates (Elith & Leathwick 2009). Un problème récurrent dans les jeux de données de distribution d'espèces qui doit être pris en compte est la présence d'autocorrélation spatiale (Dormann et al. 2007). En effet, les résultats des analyses statistiques standards sont sensibles à la présence *d'autocorrélation spatiale dans les résidus* des modèles (RSA). La présence de RSA signifie que les valeurs des résidus des modèles ne sont pas indépendantes des distances géographiques qui séparent physiquement les unités d'échantillonnage ou expérimentale dans l'espace (ex : espace euclidien à deux dimensions) (Legendre 1993).

Une des causes de la présence de RSA peut provenir de l'omission d'une variable explicative importante dans le modèle et qui possède ou induit une structure spatiale. La présence de RSA peut également découler d'une spécification inadéquate des relations fonctionnelles entre une variable explicative et la variable réponse, ou encore de l'absence de prise en compte d'un processus spatialement contagieux tel que la dispersion non-aléatoire des organismes biologiques (Dormann et al. 2007). La présence de RSA induit une augmentation des taux d'erreurs de type-I du fait de l'augmentation artificielle de la taille d'échantillonnage. La présence de RSA peut donc invalider les résultats des tests d'hypothèses (Legendre 1993). Elle peut aussi diminuer la performance prédictive des modèles (Latimer et al. 2006) et mener à une sous-estimation des erreurs associées aux prédictions et ainsi induire une illusion dans la précision des modèles (Gelfand et al. 2006).

Des efforts importants ont été consentis au cours des vingt dernières années pour développer des méthodes quantitatives capables de tenir compte de la présence de RSA lors de l'analyse statistique de données de distribution d'espèces (i.e. Legendre 1993; Banerjee *et al.* 2003; Latimer *et al.* 2006; Dormann *et al.* 2007; Beale *et al.* 2010; Dray *et al.* 2012). Toutefois, les algorithmes utilisés dans ces méthodes diffèrent souvent dans leur manière intrinsèque de modéliser l'autocorrélation spatiale et le choix d'une méthode plutôt qu'une

autre peut avoir une grande influence sur l'estimation des paramètres et l'interprétation des résultats (Dormann 2007; Kühn 2007; Bini et al. 2009). Pour résoudre ces problèmes, Beale et al. (2010) ont comparé par simulation la validité des méthodes de régression spatiale les plus couramment utilisées en écologie pour modéliser des données spatialement auto-corrélées. Leurs résultats démontrent que; 1) certaines méthodes performent mieux que d'autres; 2) les méthodes qui modélisent la dépendance spatiale directement dans le terme d'erreur du modèle performent généralement mieux en termes de taux d'erreurs de type-I et type-II que les méthodes qui incluent directement la dépendance spatiale comme variable explicative; et 3) que la seule méthode qui avait toujours un taux d'erreur de type-I inférieur à 5% dans un large éventail de conditions simulées était les modèles autorégressifs conditionnels (CAR) bayésiens. Ce dernier résultat supporte ceux de Gelfand et al. (2006) qui ont montré la flexibilité et la précision des modèles CAR bayésiens pour modéliser les patrons de distribution d'espèces sur une grille spatiale régulière. Toutefois, la principale limitation liée à la calibration des modèles CAR bayésiens réside dans l'utilisation traditionnelle des simulations *Monte Carlo Markov Chain* (MCMC) qui induit de nombreux problèmes pratiques concernant la convergence, le temps de traitement (*processing time*) et la mise en œuvre de ce type de modèle.

Dans le premier chapitre de cette thèse, j'ai donc investigué une méthode alternative aux simulations MCMC qui soit fiable, rapide et facile à mettre en œuvre pour calibrer des modèles hiérarchiques spatiaux. La contribution scientifique de ce chapitre est donc de tester la validité de ces nouvelles avancées méthodologiques comparativement aux simulations MCMC pour calibrer des modèles hiérarchiques spatiaux à partir de données de distribution d'espèces. Précisément, nous avons comparé la précision des résultats, la flexibilité et la rapidité des *integrated nested Laplace approximations* (INLA, Rue *et al.* 2009) avec les simulations MCMC dans le cas d'un modèle CAR bayésien calibré avec des données provenant d'inventaire aérien sur la distribution spatiale du caribou forestier dans l'est de la forêt boréale du Canada.

Dans ce même chapitre, nous présentons et comparons également les performances d'un modèle hiérarchique spatial alternatif au modèle CAR, avec une fonction de corrélation

Matérn (Minasny & McBratney 2005). Cette dernière approche permet de calibrer des modèles hiérarchiques spatiaux bayésiens avec des structures de covariance spatiale très générales, ce qui élargit considérablement les types de modèles spatiaux qui peuvent être pratiquement mis en œuvre sous le paradigme Bayésien.

Vers une explication écologique des gradients géographiques dans la sélection des paysages par le caribou forestier

Dans le second chapitre, nous avons utilisé INLA avec des modèles hiérarchiques spatiaux pour explorer les facteurs écologiques qui influencent la sélection hivernale des paysages par le caribou forestier dans la partie sud de son aire de répartition géographique, au sein de la zone d'exploitation commerciale de la pessière noire à mousses au Québec.

Fortin et al. (2008) ont montré que la sélection hivernale du caribou forestier pour certaines catégories d'habitat varie géographiquement avec la latitude et la longitude, ce qui suggère que des processus actifs à grande échelle spatiale influencent la façon dont les individus répondent localement à leur environnement biotique et/ou abiotique. Ce résultat vient s'ajouter aux résultats antérieures qui montrent que plusieurs espèces de grands herbivores répondent à leur environnement selon des gradients géographiques à grande échelle, par exemple, via une augmentation de leur masse corporelle avec la latitude (Ashton et al. 2000; Herfindal et al. 2006) ou encore à travers des changements dans l'intensité des relations dépendantes de la densité selon la latitude et la longitude (Post 2005).

Cependant, il n'a pas été élucidé si ces gradients latitudinaux et longitudinaux dans la sélection de certains habitats étaient le résultat de gradients à large échelle spatiale dans l'intensité des perturbations anthropiques ou bien si ces gradients coïncidaient plutôt avec des variations spatiales du climat. Identifier lequel du climat ou de l'altération humaine des paysages est l'hypothèse la plus plausible pour expliquer ce patron est essentiel car, en pratique, ces deux alternatives débouchent sur des mesures de conservation différentes. Par exemple, lutter contre les effets possibles des changements climatiques nécessite une stratégie à l'échelle mondiale avec toutes les difficultés que cela comporte, alors que la protection de certains habitats et paysages peut être menée à une échelle locale ou

régionale, par exemple à travers la création d'un réseau d'aires protégées. Les possibilités et l'échelle d'actions sont donc très différentes entre ces deux alternatives.

La première contribution scientifique du deuxième chapitre de cette thèse est donc de quantifier, en termes relatifs, le rôle joué par le climat et par les perturbations humaines dans l'existence de gradients géographiques à large échelle dans la sélection hivernale de certains habitats par le caribou forestier. Pour ce faire, nous avons utilisé un jeu de données spatiales, couvrant une large amplitude latitudinale et longitudinale, sur la présence et l'absence de réseaux de pistes de caribou forestier en hiver pour tester trois hypothèses alternatives qui pourraient expliquer la présence de gradients géographiques dans la sélection d'habitat du caribou forestier : 1) une sélection dominée par le climat qui postule que les gradients latitudinaux et longitudinaux sont en réalité l'expression de gradients climatiques sous-jacents ; 2) une sélection dominée par la distance aux routes et qui propose que le caribou forestier ajuste sa sélection de certaines catégories d'habitat en fonction de la proximité aux routes ; 3) un effet additif du climat et de la distance aux routes.

La seconde contribution scientifique de cette étude est d'évaluer, à l'échelle de la zone commerciale de la pessière noire à mousses, l'impact relatif des types de perturbations naturelles (ex : les feux) et anthropiques (ex : les coupes forestières) sur la sélection hivernale des paysages. Comme mentionné précédemment, un postulat important, qui sous-tend directement le paradigme de l'aménagement forestier écosystémique, est que la substitution des perturbations naturelles par des perturbations anthropiques de même taux et de même intensité permet de maintenir la diversité des espèces et les principales fonctions des écosystèmes (Hunter 1993). Peu d'études ont toutefois vérifié la validité de cette hypothèse pour le caribou forestier en comparant à grande échelle si l'impact des feux et des coupes forestières est effectivement équivalent. À ce titre, cette étude apporte un nouvel éclairage concernant la validité de cette hypothèse pour le caribou forestier dans le domaine de la pessière noire au Québec.

Comprendre les intéractions dans l'espace et le temps entre conservation du caribou forestier et aménagement forestier

Dans le dernier chapitre de cette thèse, nous avons simulé une étude de cas dans la région de la Côte-Nord au Québec afin d'évaluer l'efficacité économique et biologique de mesures simulées de conservation des habitats pour le caribou forestier en relation avec l'approvisionnement en matière ligneuse et le risque de feu de forêt.

Les pratiques d'aménagement forestier sur les terres publiques au Québec ont évolué au cours du temps, notamment en ce qui concerne la prise en compte des enjeux de conservation et de protection des écosystèmes forestiers. La *Loi sur les forêts* de 1986 instituait pour la première fois un ensemble de lois et règlements qui régissent les pratiques d'aménagement forestier et l'importance de concilier les usages multiples de la forêt autres que ceux liés exclusivement à l'exploitation de la matière ligneuse. Outre l'abolition des concessions forestières, les compagnies forestières devaient dorénavant signer un contrat d'approvisionnement et d'aménagement forestier (CAAF) avec le gouvernement provincial afin de pouvoir opérer sur les terres publiques. Les CAAFs définissaient de manière contractuelle les engagements réciproques du gouvernement et des industriels relativement à certaines règles et principes en aménagement forestier. Les détenteurs de CAAF se voyaient garantis un volume de bois pour l'approvisionnement de leurs usines, ce volume devant rester à l'intérieur des limites fixées par la possibilité forestière.

En 1996, la première parution du *règlement et normes d'intervention en forêt publique* (RNI) est venu renforcer les objectifs de conservation et de protection liés aux pratiques sylvicoles et d'aménagement forestier en définissant une série de mesures légales visant à 1) améliorer la protection des ressources forestières (ex : eaux, habitats fauniques, sols, productivité); 2) harmoniser l'utilisation multiple des ressources forestières; et 3) contribuer à l'aménagement durable des forêts. En 2001, d'importantes mises à jour de la *Loi sur les forêts* sont rentrées en vigueur. Parmi ces changements figurait notamment la mise en place des *objectifs de protection et de mise en valeur* (OPMV; *la Loi sur les Forêts, art. 35.6*) à l'échelle des unités d'aménagement forestier ou encore la reprise en main par le Ministère des ressources naturelles des calculs de la possibilité forestière. En

particulier, les OPMV 5 et 6, qui visent respectivement l'application de patrons de répartition spatiale des coupes adaptés à l'écologie régionale et la protection de l'habitat des espèces vulnérables ou menacées du milieu forestier, figuraient au premier plan pour la conservation de l'habitat du caribou forestier.

Depuis 2003, l'utilisation de la coupe mosaïque en forêt boréale (CMO; *RNI, art. 79.2*) est devenue prépondérante avec comme conséquence un maintien plus important de superficies non-récoltées à l'intérieur des secteurs de coupe mais aussi une dispersion plus grande des blocs de coupe à l'échelle du paysage et des unités d'aménagement. Dans le contexte de la protection de l'habitat du caribou forestier (OPMV 6; Équipe de rétablissement du caribou forestier du Québec 2008) et des principes relatifs à l'aménagement écosystémique (les patrons des coupes doivent imiter les patrons de feux; OPMV 5), l'article 25.3 de *la Loi sur les forêts* permettait aux industriels de déroger aux RNI et à la CMO en concentrant la récolte forestière dans des agglomérations de coupe. À l'échelle régionale, cela s'est notamment traduit par un morcellement des massifs de coupes.

En 2004, le rapport de la commission Coulombe sur la gestion de la forêt publique québécoise avec ses 81 recommandations a initié un tournant important dans la gestion forestière québécoise et a marqué le début vers une introduction progressive des pratiques d'aménagement écosystémique (AE). L'AE vise à diminuer les écarts entre paysages naturels et aménagés afin de maintenir à long terme la résilience et les fonctions des écosystèmes ainsi que les services sociaux et économiques que l'on en retire (voir Gauthier et al. 2009). À ce titre, l'AE reconnaît une hiérarchisation des enjeux associés au développement durable des ressources (environnement, société, économie) à savoir que l'atteinte des enjeux socio-économiques dépend avant tout de la santé et de la capacité des écosystèmes à rendre ces services (Gauthier et al. 2009). En pratique, les principes de l'AE fournissent une grille de lecture qui permet d'orienter la gestion des paysages forestiers aménagés (Bouchard et al. 2010, 2011) et qui se traduit notamment par des enjeux spécifiques en termes: 1) de structure d'âge des peuplements et de conservation des vieilles forêts; 2) d'organisation spatiale des forêts et des perturbations anthropiques; 3) de composition de la végétation; 4) de structure interne des peuplements et de bois mort; 5) de

protection des milieux humides et riverains; et 6) de conservation des espèces vulnérables et menacés d'extinction.

Le changement de paradigme vers l'AE a servi de base au gouvernement provincial pour élaborer la nouvelle stratégie sur l'aménagement durable des forêts (2010), ainsi que des règlements qui lui sont associés et qui vont prochainement entrer en vigueur. Dans la mesure où les pratiques d'aménagement forestier peuvent être antagonistes avec des objectifs de conservation du caribou forestier, il est important d'évaluer si des compromis existent entre des objectifs de conservation et des objectifs économiques liés à l'exploitation forestière.

En pratique, la majorité des mesures de conservation dans l'est du Canada s'orientent vers une gestion de l'habitat qui réduit l'empreinte écologique attribuable aux perturbations anthropiques (Ontario Woodland Caribou Recovery Team, 2008; Équipe de rétablissement du caribou forestier du Québec, 2008). Le contrôle des prédateurs est controversé et considéré comme une méthode de gestion incertaine à moyen et long terme. Pour maintenir des tailles de population de caribou forestier stables ou en croissance, Environnement Canada (2012) préconise que le pourcentage d'habitat non-perturbé qui est situé à l'intérieur des limites de répartition spatiale de chaque population (*population range*) soit au minimum de 65%. Les modalités pratiques dans l'application de mesures de conservation sont toutefois de la responsabilité des provinces et la mise en œuvre de mesures de conservation pour le caribou peut toutefois varier grandement d'une région à l'autre selon l'information disponible sur l'écologie du caribou forestier, les lois en vigueur et l'évolution des pratiques d'aménagement forestier.

Les principales mesures de conservation qui sont actuellement mises en œuvre sur la Côte-Nord visent à protéger des attributs de son habitat (ex : vieilles forêts) du développement des activités humaines (villégiature, récolte forestière, construction de chemins). Cette stratégie de protection de l'habitat du caribou forestier repose principalement sur un réseau de zones de protection temporaires, juxtaposé au réseau composé d'aires protégées permanentes (catégories III de l'UICN), et à l'intérieur desquelles aucune activité humaine

n'est autorisée (Équipe de rétablissement du caribou forestier au Québec, 2008). Ces zones temporaires de protection, appelées aussi massif de protection, ont une taille moyenne de ~100 km^2 (minimum ≈ 1 km^2, maximum ≈ 630 km^2). Leur durée de vie effective n'est toutefois pas déterminée compte tenu du manque de connaissance actuelle sur le nombre d'années nécessaires après perturbation totale pour qu'un massif forestier redevienne utilisé par le caribou. La délimitation de zones d'atténuation vient compléter la stratégie de conservation actuelle.

Toutefois, l'efficacité biologique de ces zones de conservation pour maintenir à long terme des populations stables ou en croissance de caribou forestier dans la région n'est pas connue dans un contexte où le régime des feux interagit spatialement avec un régime de coupes forestières. L'influence de ces zones de conservation sur les niveaux de récolte et de coûts liés aux activités d'aménagement forestier sont également peu documentés ce qui rend l'évaluation de l'efficacité d'une telle stratégie de conservation difficile, tant d'un point de vue biologique qu'économique. Dans ce contexte, le but de cette étude était d'explorer dans l'espace et le temps l'efficacité écologique et économique de mesures de conservation pour le caribou forestier qui sont inspirées de la réalité et ce dans un contexte de régimes multiples de perturbation.

Pour ce faire, nous avons mis en œuvre une expérience factorielle à partir d'un modèle de simulation des paysages spatialement explicite pour quantifier les effets *i)* de mesures de protection des habitats pour le caribou, *ii)* de la foresterie industrielle, *iii)* des régimes de feu, *iv)* ainsi que leurs interactions, sur le taux de recrutement des faons (nombre de faons/100 femelles) de caribou forestier et sur les coûts économiques reliés à l'aménagement forestier. La contribution scientifique de cette dernière étude est de mieux comprendre les interactions spatiales complexes qui existent entre ces différents processus afin de développer des stratégies de conservation pour le caribou forestier qui soient efficaces. Dans la mesure où le cadre législatif et la mise en oeuvre de nouvelles mesures d'aménagement écosystémique et de conservation de l'habitat du caribou forestier évoluent rapidement (Équipe de rétablissement du caribou forestier du Québec 2013), le type d'approche utilisée dans cette étude ainsi que les résultats qui en découlent ont le potentiel

d'éclairer la mise en œuvre conjointe de mesures de gestion et de conservation des paysages forestiers qui soient plus durables.

Références

Ashton, K.G., Tracy, M.C. & Queiroz, A.D. (2000) Is Bergmann's Rule valid for mammals? *American Naturalist* 156: 390-415.

Banerjee, S., Carlin, B. P. & Gelfand, A. (2003) Hierarchical modeling and analysis for spatial data. Chapman and Hall, Boca Raton, Florida, USA.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51-57.

Beale, C. M., Lennon, J. J., Yearsley, J. M., Brewer, M. J. & Elston, D. A. (2010) Regression analysis of spatial data. *Ecology Letters* 13: 246-264.

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., Aparicio, A., Araújo, M.B., Baselga, A., Beck, J., Bellocq, M.I., Böhning-Gaese, K., Borges, P.A.V., Castro-Parga, I., Chey, V.K., Chown, S.L., de Marco, P., Dobkin, D.S., Ferrer-Castán, D., Field, R., Filloy, J., Fleishman, E., Gómez, J.F., Hortal, J., Iverson, J.B., Kerr, J.T., Kissling, W.D., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Morales-Castilla, I., Moreno, J.C., Oberdorff, T., Olalla-Tárraga, M.Á., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.Á., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N.J., Terribile, L.C., Vetaas, O.R. & Hawkins, B.A. (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography* 32 : 193–204.

Bouchard, M., Déry, S., Jacqmain, H., Jetté, J.-P. & Leblanc, M. (2010). Intégration des enjeux écologiques dans les plans d'aménagement forestier intégré. Partie I — Analyse des enjeux (version préliminaire 1.0), gouvernement du Québec, ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts, 117 p.

Bouchard, M., Déry, S., Jacqmain, H., Jetté, J.-P., Leblanc, M., Villeneuve, N., Bertrand, N. & Pâquet, J. (2011). Intégration des enjeux écologiques dans les plans d'aménagement forestier intégré. Partie II – Élaboration de solutions aux enjeux, version préliminaire 1.1, gouvernement du Québec, ministère des Ressources naturelles et de la Faune, Direction de l'aménagement et de l'environnement forestiers, 124 p.

Boulanger, Y., Gauthier, S., Gray, D. R., Le Goff, H., Lefort, P., & Morissette, J. (2013) Fire regime zonation under current and future climate over eastern Canada. *Ecological Applications* 23: 904-923.

Courtois, R., Ouellet, J.-P., Gingras, A., Dussault, C., Breton, L. & Maltais, J. (2003) Historical changes and current distribution of caribou in Québec. *Canadian Field-Naturalist* 117:399-414.

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: 491-498.

Dormann, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kuhn, I., Ohlemuller, R., Peres-Neto, P. R., Reineking, B., Schroder, B., Schurr, F. M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609-628.

Dray, S., Pélissier, R., Couteron, P., Fortin, M. J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F.G., De Caceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J. & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82: 257-275.

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.

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 + 138pp.

Équipe de rétablissement du caribou forestier du Québec (2008) Plan de rétablissement du caribou forestier (*Rangifer tarandus*) au Québec 2005-2012. Ministère des Ressources naturelles et de la Faune, Faune Québec, Direction de l'expertise sur la faune et des habitats, Canada.

Équipe de rétablissement du caribou forestier du Québec (2013) Lignes directrices pour l'aménagement de l'habitat du caribou forestier (*Rangifer tarandus caribou*), produit pour le compte du ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, 24 p. + 1 annexe.

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: 419-434.

Fortin, D., Courtois, R., Etcheverry, P., Dussault, C. & Gingras, A. (2008) Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. *Journal of Applied Ecology* 45 : 1392-1400.

Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. (2009) Ecosystem management in the boreal forest. Presses de l'Université du Québec, Québec, QC, Canada.

Gelfand, A. E., Silander, J. A., Wu, S. S., Latimer, A., Lewis, P. O., Rebelo, A. G. & Holder, M. (2006) Explaining Species Distribution Patterns through Hierarchical Modeling. *Bayesian Analysis* 1: 41-91.

Government of Quebec (2010) Loi sur l'aménagement durable du territoire forestier. http://www2.publicationsduquebec.gouv.qc.ca/dynamicSearch/telecharge.php?type=2&file=/A_18_1/A18_1.html [Accessed on May 13, 2012].

Herfindal I, Solberg E, Sæther B-E, Høgda K, Andersen R (2006) Environmental phenology and geographical gradients in moose body mass. *Oecologia* 150: 213-224.

Hunter Jr ML (1993) Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* 65: 115-120.

Kühn, I. (2007). Incorporating spatial autocorrelation may invert observed patterns. *Diversity and Distributions*, **13(1)**, 66-69.

Latimer, A. M., Wu, S. S., Gelfand, A. E. & Silander, J. A. (2006) Building statistical models to analyze species distributions. *Ecological Applications* 16: 33-50.

Legendre, P. (1993) Spatial autocorrelation - trouble or new paradigm? *Ecology* 74: 1659-1673.

Minasny, B. & McBratney, A. B. (2005) The Matérn function as a general model for soil variograms. *Geoderma* 128: 192-207.

Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006) Integrating economic costs into conservation planning. *Trends in Ecology & Evolution* 21: 681-687.

Ontario Woodland Caribou Recovery Team. 2008. Woodland Caribou (*Rangifer tarandus caribou*) (Forest-dwelling, Boreal Population) in Ontario. Prepared for the Ontario Ministry of Natural Resources, Peterborough, Ontario. 93 pp..

Post E (2005) Large-scale spatial gradients in herbivore population dynamics. *Ecology* 86: 2320-2328.

Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B-Statistical Methodology* 71: 319-392.

Sharma S, Couturier S, Côté, S.D. (2009) Impacts of climate change on the seasonal distribution of migratory caribou. *Global Change Biology* 15, 2549-2562.

Sorensen, T., McLoughlin, P. D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., & Boutin, S. (2008) Determining sustainable levels of cumulative effects for boreal caribou. *The Journal of Wildlife Management* 72 : 900-905.

Thuiller W (2007) Biodiversity: Climate change and the ecologist. *Nature* 448: 550-552.

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: 568-579.

CHAPITRE 1:

HIERARCHICAL ANALYSIS OF SPATIALLY AUTOCORRELATED ECOLOGICAL DATA USING INTEGRATED NESTED LAPLACE APPROXIMATION (INLA)

JULIEN BEGUIN, SARA MARTINO, HÅVARD RUE & STEVEN G. CUMMING

Résumé

L'analyse spatiale de données écologiques est incontournable pour résoudre de nombreuses questions contemporaines en écologie. L'utilisation des méthodes bayésiennes pour calibrer des modèles spatialement explicites a reçu une attention croissante de la part des écologistes depuis que les méthodes basées sur les simulations utilisant *Monte Carlo Markov Chain* (MCMC) ont été rendues librement et facilement accessibles. Bien que les simulations par MCMC offrent une plate-forme flexible pour modéliser un large spectre de jeux de données écologiques, ces méthodes s'accompagnent également de nombreux problèmes en ce qui à trait à la convergence des modèles, à leur programmation et au temps nécessaire pour obtenir les résultats. Dans cette étude, nous introduisons, pour les écologistes, une procédure alternative capable de calibrer des modèles hiérarchiques spatiaux bayésiens avec des structures spatiales de covariance très générales. Cette procédure utilise les *approximations de Laplace nichées et intégrées* (INLA) comme méthode alternative aux simulations par MCMC. Nous montrons, grâce à une étude de cas utilisant un modèle de distribution d'espèce calibré sur une grille régulière avec des données binaires, que la mise en œuvre d'un modèle hiérarchique spatial bayésien avec INLA ne requiert pas de compétences avancées en programmation, produit des résultats aussi précis que par MCMC et est rapide (ex : de l'ordre de quelques secondes pour des jeux de données de taille petite à modérée). Les modèles hiérarchiques spatiaux bayésiens testés dans cette étude ont, premièrement, enlevé de manière efficace l'autocorrélation spatiale présente dans les résidus des modèles et, deuxièmement, évalué justement l'incertitude des paramètres estimés ainsi que les prédictions. La rapidité de la méthode INLA a permis, d'une part, de diminuer significativement le temps pour faire converger les modèles et, d'autre part, de réaliser dans des temps raisonnables des analyses de sensibilité sur les *priors* ainsi que des tests de validations croisées, ce qui ultimement augmente la transparence des modèles.

Summary

Spatial analysis of ecological data is central to many interesting questions in ecology. Bayesian implementation of spatially explicit models has received increasing attention from ecologists as Monte Carlo Markov Chain (MCMC) methods have become freely accessible. MCMC simulations offer a flexible framework for modelling extensive ecological data, but they also come with a wide range of problems regarding convergence, processing time and implementation. We introduce to ecologists an alternative procedure for fitting Bayesian hierarchical spatial models (BHSM) with quite general spatial covariance structures. This procedure uses integrated nested Laplace approximations (INLA) as an alternative to MCMC. We show, using a case study of species distribution model with binary areal data, that implementing BHSM with INLA does not require advanced programming skills, yields accurate results compared with MCMC and is rapid (e.g. a few seconds with small to moderate data sets). BHSMs efficiently removed spatial autocorrelation in the residuals and fairly evaluated uncertainty in parameter estimates and predictions. The rapidity of INLA significantly decreased the processing time and allowed both sensitivity analyses on priors and cross-validation tests to be performed within a reasonable amount of time, which ultimately increased model transparency.

Introduction

Spatial analysis of ecological data is central to most contemporary issues in applied ecology. Species distribution models provide key information regarding species–environment relationships, and particularly about how environmental stressors limit species distributions (Elith & Leathwick 2009). In the global context of increasing human impacts on ecosystems, predictions derived from such models can inform management plans for endangered species (Cabeza *et al.* 2004), and assessments of distributions under future land-use (Bomhard *et al.* 2005) and climate (Thuiller 2003) scenarios. Unfortunately, acquiring reliable inferences and predictions from statistical analysis of distributional data is not straightforward. One problem that must be addressed is spatial autocorrelation. Analyses of species distributions are sensitive to spatial dependency in model residuals, or in other words, residual spatial autocorrelation (RSA; Latimer *et al.* 2006). RSA occurs when model residuals at nearby locations are not independent (Legendre 1993). RSA may arise from missing covariates that have or induce spatial structure, from incorrect specification of the functional relationship between a covariate and the response, or from neglecting to account for a spatially contagious process such as non-random dispersal of individuals. RSA is associated with biased Type-I error estimates owing to inflation of the effective sample size, which invalidates standard hypothesis tests (Legendre 1993). RSA may also reduce model performance (Latimer *et al.* 2006) and lead to underestimation of prediction errors (Gelfand *et al.* 2006). Hence, RSA should be avoided by correct model specification. In practice, though, important environmental covariates are often neglected because they have not been identified or are unmeasured.

Several statistical methods have emerged for modelling spatial data while accounting for RSA (e.g. see Dormann *et al.* 2007 for frequentist methods and Banerjee, Carlin & Gelfand 2003 for Bayesian methods). With freely available Monte Carlo Markov Chain (MCMC) methods, Bayesian implementation of spatially explicit models has received increasing attention from ecologists. The conditional autoregressive (CAR) model is one example of such models that is now routinely used in ecology for modelling spatial association in data sampled within areal units (Latimer *et al.* 2006), along roads (Thogmartin, Sauer & Knutson 2004) or transects (Aing *et al.* 2011) or at points (Haas *et al.* 2011). In the context

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of spatial regression, Beale *et al.* (2010) showed that Gaussian Bayesian CAR models fitted using MCMC yielded precise and unbiased parameter estimates with low Type-I and Type-II errors. While they are always possible to implement in principle, MCMC algorithms applied to complex hierarchical spatial models have a wide range of problems related to convergence and computation time: the fitting procedure is not guaranteed to converge or may converge very slowly. Moreover, implementation of the algorithms can prove problematic in itself, especially for users who are not expert in programming.

Integrated nested Laplace approximation (INLA) is a recent alternative to MCMC for fitting a large class of Bayesian models such as latent Gaussian models (Rue, Martino & Chopin 2009). Latent Gaussian models can account for hierarchical structure and non-Gaussian errors, as well as spatial and temporal autocorrelation (see INLA section). In fitting these models, INLA substitutes accurate, deterministic approximations to posterior marginal distributions in place of long MCMC simulations, thereby gaining in speed. The quality of such approximations is extremely high, as shown by comparisons with long MCMC runs (Rue, Martino & Chopin 2009). INLA has two main advantages over MCMC techniques. The first and most outstanding is computational: results can be obtained much faster than with a well-built MCMC-sampler. The INLA algorithm is naturally parallelized, thus making it possible to exploit the new computing trend of having multicore processors. The second advantage is that INLA permits a great deal of automation and, in practice, can be almost used as a black box to analyse latent Gaussian models. This second point is especially important in applied communities where programming expertise is limited. An R-INLA library with a user-friendly R interface (R Development Core Team 2011) is freely available at http://www.r-inla.org.

Although INLA is accurate, fast and freely available, it is still little known to ecologists. The first aim of this study is therefore to introduce this recent procedure for fitting spatially explicit hierarchical models to ecological data. To do so, we first compare results obtained with a Bayesian CAR model fitted with MCMC and INLA using spatial data on the distribution of forest-dwelling or boreal woodland caribou (*Rangifer tarandus caribou*) in eastern Canada. Second, we present and compare the performance of an alternative

hierarchical spatial model using a flexible approach with a Matérn correlation function (Minasny & McBratney 2005). Using the INLA-R library, we show how these models can be easily fitted, even by non-expert programmers. We conclude with discussion of specific issues regarding spatial autocorrelation, the interpretation of latent spatial patterns, and the parameterization of spatial random effects in hierarchical models.

Integrated nested Laplace approximation

In the following description, we assumed some familiarity with Bayesian analyses and the use of likelihood functions. For additional description of these notions, see Hilborn & Mangel (1997) or Bolker (2008). Based upon Bayes' theorem, Bayesian analyses combine prior probability distributions with likelihood to target posterior probability distributions of parameters. In this study, we consider a particular class of Bayesian hierarchical models called latent Gaussian models. In this class of models, a latent Gaussian field x is partially observed through data y. Depending on the structure and the type of model considered, the latent field x may include, simultaneously or not, parameters associated with linear predictors (e.g. linear regression models), spline functions (e.g. additive models) and nonspatial or⁄and spatial random effects (e.g. hierarchical spatial models). Moreover, the probability distribution of y can follow any distribution belonging to the exponential family such as Gaussian, Poisson, Binomial, Beta and many others. The prior density of the latent field $\pi(x|\theta)$ and the likelihood of the data $\pi(y|x,\theta)$ are governed by a vector of hyperparameters θ with prior density $\pi(\theta)$. In practice, we are often interested to make inference about the posterior marginal distribution of parameters such as:

$$\pi(x,\theta|y) \propto \pi(y|x,\theta)\,\pi(x|\theta)\,\pi(\theta)$$

Getting marginal distribution of parameters, however, is almost always analytically intractable because the likelihood often is not Gaussian and the latent field is of high dimension. Stochastic sampling with MCMC methods (e.g. see Banerjee, Carlin & Gelfand 2003; Gelman & Hill 2007) can be used to solve this issue. In theory, MCMC algorithms give exact results. They also are flexible for a wide range of models. One practical limitation of MCMC for fitting spatial models, however, is its low computational speed.

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Processing time can be sufficiently long so as to preclude the analysis of even small spatial data sets. Moreover, computational demands can make impractical the use of sensitivity analyses on priors and cross-validation tests. This can lead to poor interpretation of the results.

As an alternative to MCMC, INLA substitutes stochastic sampling with deterministic approximations based on a clever use of the Laplace approximation and on numerical integration. INLA can be used when the latent field x is a Markov field, which means that the latent field is endowed with a conditional independent structure, for a detailed description of Gaussian Markov field see Rue & Held (2005). In addition, INLA is most useful when the main interest lies in posterior marginal distributions $\tilde{\pi}(\theta_j|\mathbf{y})$ and $\tilde{\pi}(x_j|\mathbf{y})$. This is the case when, for example, assessing the effect of covariates is the goal. We give here a short description of the INLA procedure and refer the interested reader to Rue, Martino & Chopin (2009). The INLA procedure consists of three successive steps. First, an approximation of the marginal posteriors of hyperparameters $\tilde{\pi}(\boldsymbol{\theta}|\mathbf{y})$ is computed using Laplace approximation. The main use of this approximation is to select good estimation points to integrate out the uncertainty with respect to $\boldsymbol{\theta}$ when approximating the posterior marginals of each parameter x_i. A key feature here is to avoid representing $\tilde{\pi}(\boldsymbol{\theta}|\mathbf{y})$ parametrically, which allows more flexibility together with reducing computational demands. The second step consists of approximating the posterior marginal for the xi conditioned on selected values of $\boldsymbol{\theta}$, $\tilde{\pi}(x_i|\boldsymbol{\theta},\mathbf{y})$, using again Laplace approximations. Finally, an approximation to $\tilde{\pi}(x_i|\mathbf{y})$ is computed via numerical integration as:

$$\tilde{\pi}(x_i|\mathbf{y}) = \int \tilde{\pi}(x_i|\boldsymbol{\theta},\mathbf{y})\,\tilde{\pi}(\boldsymbol{\theta}|\mathbf{y})\,\mathrm{d}\boldsymbol{\theta} \; = \sum_j \tilde{\pi}\big(x_i|\theta_j,\mathbf{y}\big)\,\tilde{\pi}\big(\theta_j|\mathbf{y}\big)\,\Delta_j \qquad \text{[Eqn. 1]}$$

Where the points θ_j are selected in the first step of the INLA algorithm and Δ_j are associated weights. When the number of hyperparameters is small (e.g. <6), as is the case in most ecological applications, the computation of these approximations is very fast and accurate, as shown by long-run comparisons with MCMC (see Rue, Martino & Chopin 2009). These computational advantages and the fact that there is a user-friendly software

make INLA an appealing alternative for latent Gaussian models, including generalized linear (or additive) mixed models, time-series models, geoadditive models and state-space models, all of which are currently applied more or less commonly to the analysis of ecological data.

Case study: Boreal woodland caribou in the boreal forest of eastern Canada

We illustrate the use of INLA in the context of hierarchical spatial modelling with spatially autocorrelated distributional data. First, we compared the performance of INLA with MCMC using an intrinsic spatial CAR model. For the MCMC method, we used a Gibbs sampler that was implemented in WinBUGS (available online at http://www.mrcbsu.cam.ac.uk/bugs/winbugs/contents.shtml). Second, we show an alternative hierarchical spatial method, which uses a Matérn correlation function to account for spatial associations among units. Matérn spatial correlation models are not supported in WinBugs, so we only present these result using INLA. Overall, the purpose of these comparisons is to show that powerful alternatives to MCMC exist for fitting a wide range of spatially explicit hierarchical models in ecology and evolution. All models using INLA were fitted in R v2.14.1 using the R-INLA library. Data and R-codes are available in Appendix 1.1.

Data

Our case study consists of species distribution data obtained in 1999 from an extensive aerial winter survey of forest-dwelling caribou (*Rangifer tarandus caribou*) in a region of 42 071 km2 located in the boreal forest of eastern Québec, Canada (Courtois *et al.* 2003). This region and data are a subset of those studied by Fortin *et al.* (2008). The observational units for this study are the presences or absences of intensive caribou snow track networks (ICTN). An ICTN indicates areas that were used briefly and intensively by a small group of caribou for foraging or shelter. A total of 232 ICTNs were detected and mapped by an exhaustive winter aerial survey consisting of a dense grid of fixed-wing transects backed up by helicopter spot-checks (see Courtois *et al.* 2003 for details). The mean size of an ICTN

is 0.53 km^2 (SE, ± 0.06 km^2). ICTN locations were taken to be their centroids. The probability of detection given presence is high (>90%), owing to strong contrasts between ICTN and adjacent undisturbed snow surfaces (Courtois *et al.* 2003). Given the high detectability of ICTN and the intensity of sampling effort, false-positives and false-negatives can be ignored. We initially selected 13 covariates that could potentially influence the probability of ICTN presence (Table 1.1).

Table 1.1. Environmental variables used as predictors in our study. Minimum, mean and maximum values of each explanatory variable, at the scale of 100 km2 grid cells, are presented for the entire region. Variables in bold were retained in the final candidate model for each statistical method.

Environmental variables	Minimum	Mean	Maximum
X-coordinates (km)	-	-	-
Y-coordinates (km)	-	-	-
Wetlands (km^2)	0,1	2,8	23,1
Water bodies (km^2)	1,9	14,0	87,8
Lichen woodland (km^2) (WoodLichen in Fig. 1.3)	0	3,6	27,8
Open lichen (km^2) (OpenLichen in Fig. 1.3)	0	3,5	32,2
Coniferous Forests (km^2)	0	54,1	91,5
Deciduous Forests (km^2)	0	3,5	44,7
Wildfire (km^2)	0	9,8	82,2
Logging (km^2)	0	19,9	83,1
Other land cover (km^2)	0	3,1	43,4
Road density (km/km^2)	0	0,5	5,1
Winter mean temperature (˚C)	-18,91	-16,5	-12,67
Winter total precipitation (mm)	47	60	73
Altitude (m)	239	500	879

These covariates have been obtained from several data sources, including digital forest inventories, interpolated climate data (McKenney *et al.* 2006) and a 0.75 arc-second resolution Digital Elevation Model (available online at http://www.geobase.ca/geobase/fr/data/cded/description.html). Forested and non-forested variables were classified from updated forest inventory mapsheets. The classification used is described in Appendix 2.1. (Note: environmental variables "Open lichen", "Deciduous forests", and "Coniferous forests" in Table 1.1. refer to variables "Lichen heaths",

"Deciduous + Mixed deciduous stands", and "all other coniferous stand types combined" in Appendix 2.1, respectively). Road density included all types of roads from paved to bush trails. Wildfire and logging variables were classified based on the disturbance type and vegetation height class (see Table 2.1.). Classifying disturbance events based on the time since disturbance can yield very different vegetation profiles (i.e. height and density) according to the level of site productivity and regeneration success, which can vary from one stand to another. It seems intuitive to assume that caribou respond more to the vegetation structure left after a disturbance event than the variable "time since disturbance" itself. The spatial resolution of covariates was 500 m^2 for elevation, 8 ha for forest inventory attributes and 100 km^2 for climate data. All attributes were calculated as total areas or averages over a common 100 km^2 grid defined by the climate data (see Table 1.1). A linear model of co-regionalization revealed that a grain size of 100 km^2 was appropriate to delineate homogeneous spatial units within the study region. The chosen spatial grid and grain size also corresponds to that of our interpolated climate data, the covariate of lowest spatial resolution. Hereafter, each elementary unit of this grid is referred to as a cell (N = 465). Caribou presence⁄absence data within cells, however, was calculated for a 1-km^2 resolution subgrid. This resolution corresponds to roughly twice the mean area of an ICTN (see Fig. 1.1 below).
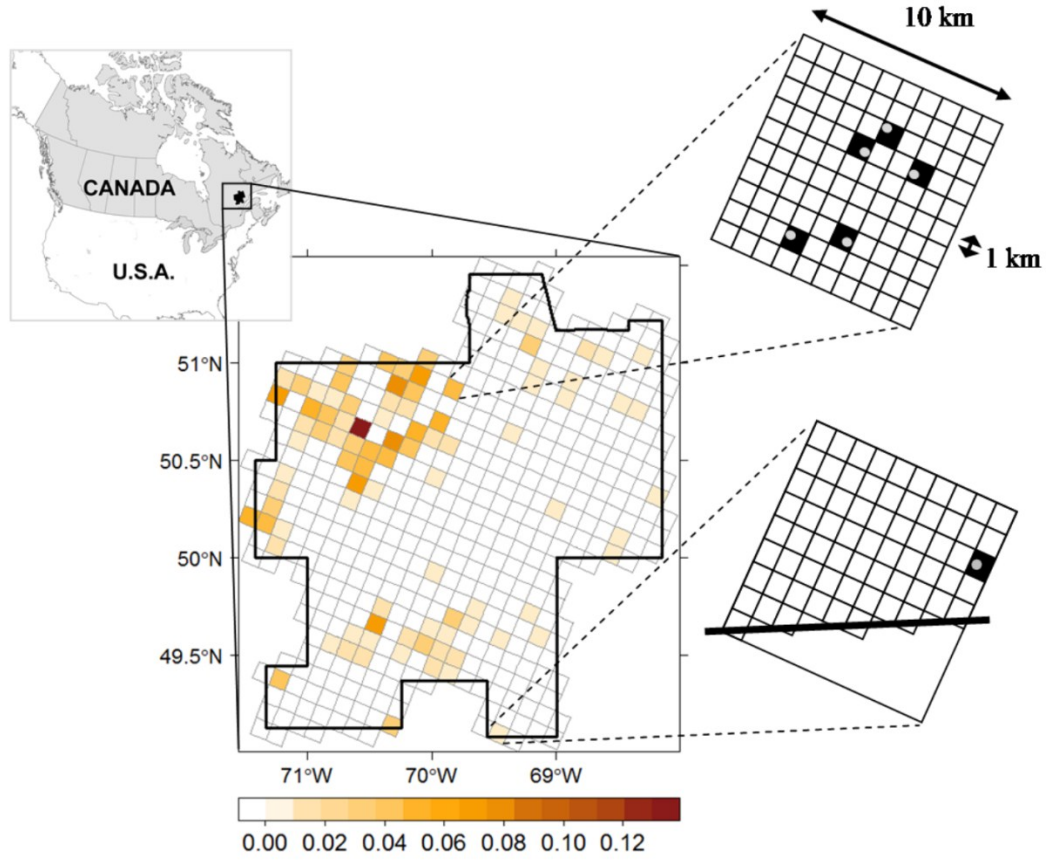
Figure 1.1. Study region located in the boreal forest of eastern Canada. Bold black lines in the middle-panel delineate boundaries of the aerial survey. Colours define the proportion of intensive winter track networks of boreal woodland caribou (ICTN) in each of 465 cells of 100-km2. The right-side panel highlights two spatial unit structures. The 100-km2 grid represents spatial units at which environmental variables are evaluated, and the 1-km2 grid represents spatial units where the presence (black squares, with grey ICTN centroids inside) or absence (white squares) of ICTN was detected. See text for further description.

Statistical models

Let n_i be the number of 1-km2 subcells within the ith cell, and Y_i the number of these subcells where the presence of ICTN is observed. We assume Y_i to be a binomial random variable and have modelled the probability p_i of ICTN presence within cells using a logit link function and the following generic model:

$$Y \sim \text{Binomial}\ (n_i, p_i)$$

$$\text{logit}(p_i)\ =\ \boldsymbol{\beta X}_i + f(s_i) \qquad\qquad \text{[Eqn. 2]}$$

Here, X_i is the vector of covariates for cell i, and $\boldsymbol{\beta}$ is the vector of parameters to be estimated. The two hierarchical spatial models considered in this study only differ in their intrinsic way of defining the spatial random effect $f(s)$. A spatial random effect is used to model dependence among neighbouring cells that is not explained by the covariates. All models assumed a vague Gaussian prior for the regression parameters $\boldsymbol{\beta} \sim \mathcal{N}$ (mean = 0, precision = 0.001), where precision = 1 / variance. For the binomial intrinsic CAR model fitted with INLA, the prior for the spatial random effect is defined conditionally as:

$$f_s(s)|f_s(s'), s \neq s', \lambda_s \sim \mathcal{N}\left(\frac{1}{n_s}\sum_{s \sim s'} f_s(s'), \frac{1}{n_s\lambda_s}\right)$$

where $s \sim s'$ indicates that the two cells s and s' are neighbours and n_s is the number of neighbours of cell s.. We defined two cells to be neighbours if they directly share a single boundary point. The unknown precision hyperparameter λ_s controls the smoothness of the spatial random effect and the prior is defined on a logarithmic scale such as it follows a logGamma (shape = 24.47, scale = 0.001) distribution (see the following section on prior choices). Further details of this model can be found in chapter 3 in Rue & Held (2005). The spatial random effect in the Matérn model is a Markov representation on a regular grid of a continuous Gaussian field with a Matérn covariance function. The Matérn function offers a flexible way of modelling spatial dependence among units as it includes the exponential and squared exponential covariance functions as special cases (see section 2.1.3. in Banerjee, Carlin & Gelfand 2003 or Minasny & McBratney 2005 for details). The correlation function in the Matérn model is defined as:

$$Corr(d) \propto (\kappa d)^\nu\, K_\nu(\kappa d)$$

Where d is the Euclidean distance, $K_\nu()$ is the Bessel function of order ν. The range is defined to be $\sqrt{8}/\kappa$ and it is the distance at which two cells are practically uncorrelated. The Matérn model has two hyperparameters: the precision of the spatial random effect and the range as defined above. As it is a difficult task to estimate simultaneously both range and precision parameters, we fixed the range to be five times the distance between two neighbouring cells. This value for the range was meant to capture the fine scale spatial

association among cells. As for the CAR model, the precision hyperparameter is defined internally on a logarithmic scale and we assigned it a logGamma (shape = 23.36, scale = 0.001) prior. The Matérn covariance function implies a dense covariance matrix that greatly increases computational demands and processing time. The INLA software uses a Markov representation of the Matérn field that has been introduced by Lindgren, Lindstrøm & Rue (2011). The Markov representation offers several computational advantages and greatly reduces the running time to fit such model. The description of such Markov representation is beyond the scope of this study and the interested reader is referred to Lindgren, Lindstrøm & Rue (2011). Finally, to ensure parameter identifiability, a sum-to-zero constraint is imposed on $f(s)$ in all cases.

Variable selection and prior choices

Logistic, CAR and Matérn models were fit using the same design matrix X_i of environmental covariates, which were selected from the initial set of 13 covariates by a preliminary screening process. Selection was carried out by fitting a full logistic model without spatial random effect and then calculating variance inflation factors (VIF) as a test for multicollinearity (Zuur *et al.* 2009). Covariates with VIF > 4 were removed one-by-one using a backwards, stepwise procedure. We then fit every model with the same eight covariates using linear effects on the logit scale (Table 1.1). For the CAR and Matérn models, the choice of the shape parameter for the precision of the spatially structured effect $f(s)$ determines the smoothness of the spatial effect and, through this, the spatial scale at which it operates. Misspecification of this parameter can lead to poor interpretation of the results (e.g. overfitting), so special care must be taken. To avoid pitfalls, we manually investigated the sensitivity of the results for a wide range of shape parameter values. In particular, we investigated the effect of various shape parameter values on coefficient estimates and credible intervals of explanatory variables, deviance information criterion (DIC), the number of effective parameters and the number of effective replicates. As model comparisons that are based on DIC can underpenalize for model complexity and thus encourage overfitting (Plummer 2008), we retained values of the shape parameters such that the ratio of data/parameters was always >20 (Burnham & Anderson, 2002).

Model outputs

For each fitted model, we calculated the mean predicted value of ICTN presence in each cell (with 95% credible intervals) and estimated RSA using variograms. We compared inferential properties among models using parameter estimates and their credible limits. We assessed model goodness-of-fit by calculating the Pearson's correlation coefficient (r) between predicted values and observed proportions of ICTN presence at the cell level. Finally, we used 'leave-one-out' cross-validation to assess the predictive power of each model, based on the conditional predictive ordinate (CPO) statistic (Held, Schrödle & Rue 2010). Following Held, Schrödle & Rue (2010), the CPO value for the ith cell is defined as $\text{CPO}_i = \pi(y_{i,obs} | y_{-(i),obs})$, where $y_{i,obs}$ is the binomial outcome of the ICTN presence for cell i, and $y_{-(i),obs}$ denotes the data without the ith cell. The number of cells is 465. We used the mean logarithmic-CPO$_i$ defined as:

$$\overline{\text{LCPO}} = -\frac{1}{465} \sum_i \log(\text{CPO}_i) \qquad [\text{Eqn. 3}]$$

The lower the $\overline{\text{LCPO}}$ for a model, the better is its predictive power.

Results

Conditional autoregressive and Matérn models adequately removed RSA present in the nonspatial logistic model (Fig. 1.2).
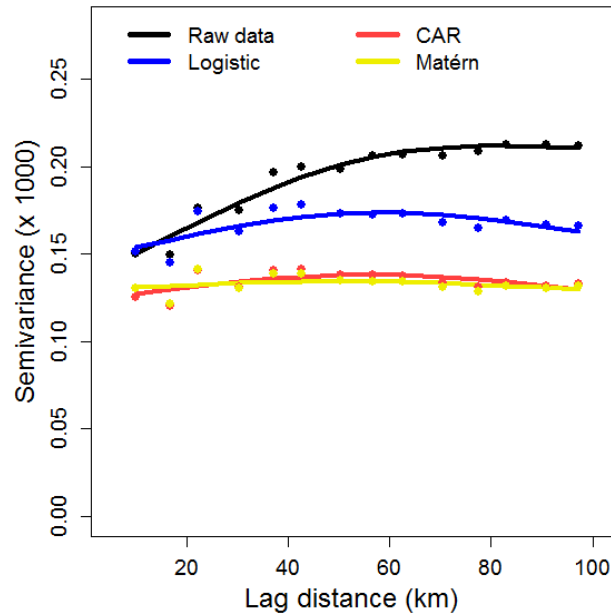
Figure 1.2. Spatial variograms of (i) the raw data; (ii) residuals of the nonspatial logistic model; (iii) residuals of the hierarchical conditional autoregressive (CAR) model; and (iv) residuals of the spatial model with a Matérn correlation function. Note: A likelihood-ratio (LR) test between the following two models shows that residuals of logistic model are spatially autocorrelated (LR = 10.1, P = 0.007): model 1: Semi-variance = β_0. model 2: Semi-variance = $\beta_0 + \beta_1$ distance + β_2 distance^2.

We detect no difference in parameter estimates for the Bayesian CAR model using MCMC vs. INLA approaches (Fig. 1.3). Nor did we find any significant difference in parameter estimates between Matérn and CAR models fitted with INLA (Fig. 1.3). When fitted with MCMC (100 000 iterations, three chains), the CAR model took several hours to converge, whereas INLA took c. 5 s. Estimation of the Matérn model with INLA was also a matter of seconds. As expected, results of hierarchical spatial model outcomes are sensitive to specification of the shape parameter (Fig. 1.4, Appendix 1.2). The shape parameter governs the smoothness of the spatial random effect: low values (e.g. uninformative priors) mirror spatial associations at short distances, whereas high values mirror spatial correlation at large distances (Fig. 1.4).
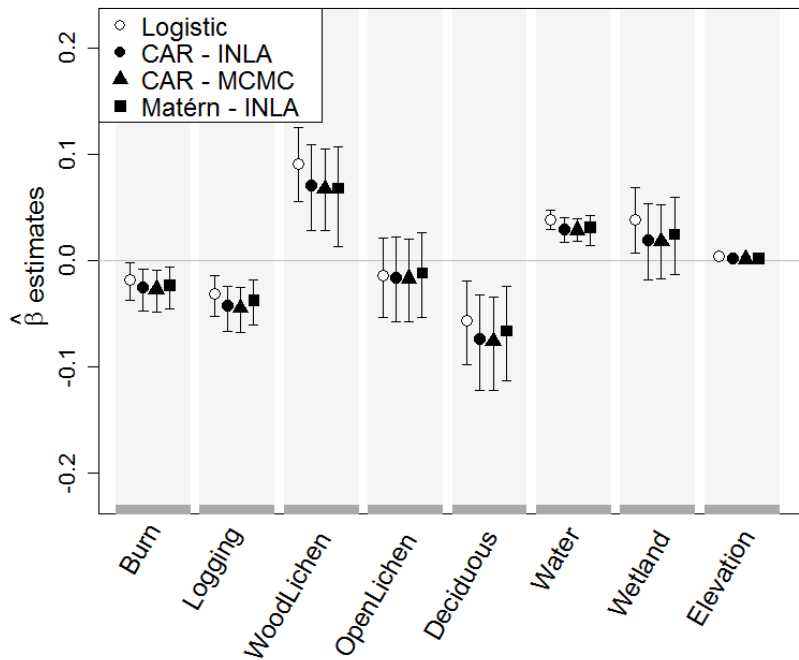
Figure 1.3. Parameter estimates (± 95% credible intervals) of every environmental variable used for each statistical method in this study. See Table 1.1 for a description of each variable.

Our result shows that accounting for autocorrelation at short distances comes with the cost of increasing number of estimated parameters, which in turn increases the risk of overfitting (Fig. 1.4). We found that DIC-based comparisons underpenalized for model complexity and encouraged overfitting (Fig. 1.4). To avoid this issue and to balance the amount of information contained in the data with the number of estimated parameters, we selected a shape parameter so that the number of effective replicates was greater than, but close to, 20 (Fig. 1.4). Lower values of effective replicates encouraged overfitting, while higher values only mirrored spatial trend at broad scales (Fig. 1.4). When values of the shape parameter are 24.5, the binomial CAR model no longer differs from a nonspatial logistic model.
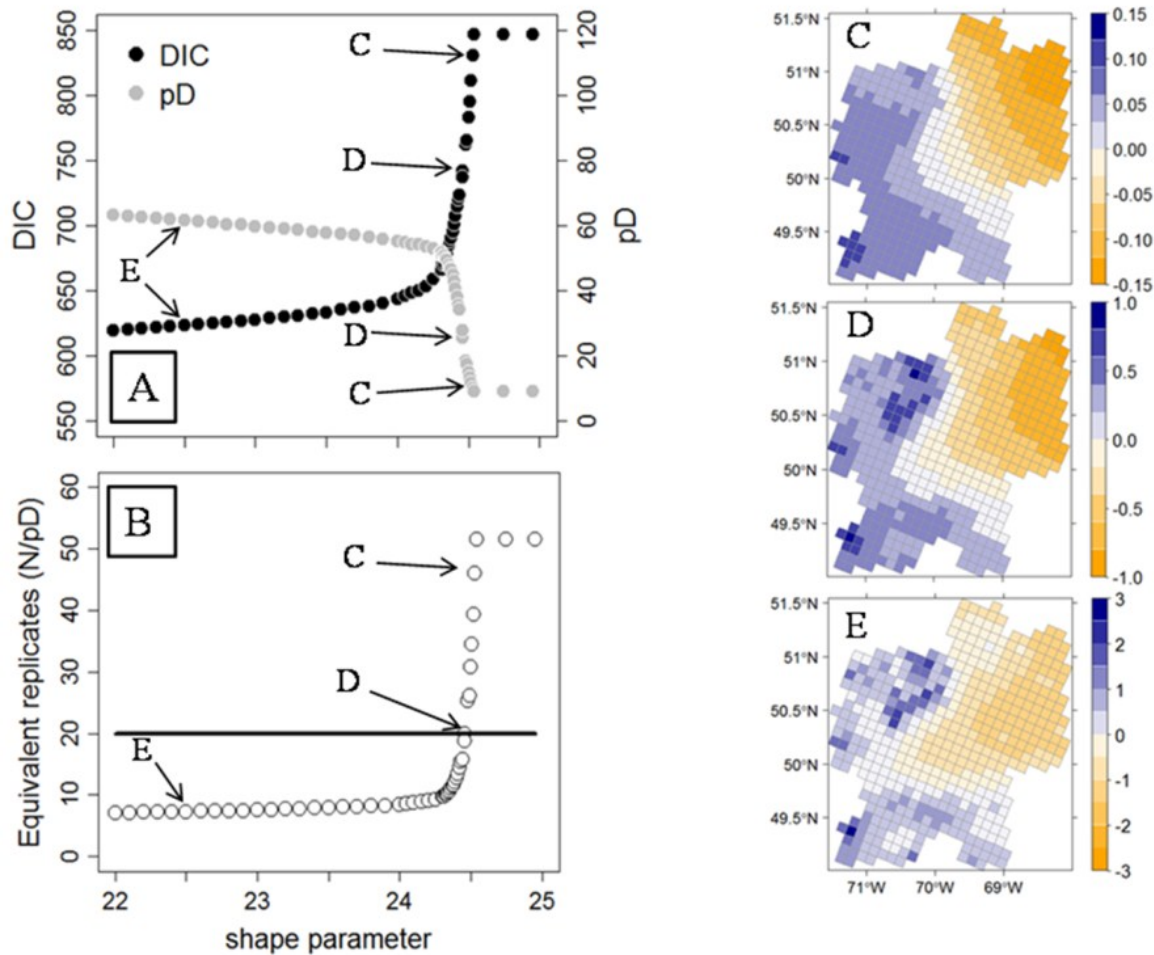
Figure 1.4. Left panel: sensitivity analyses for Bayesian CAR model showing the effect of different values of the shape parameter on A) deviance information criteria (DIC) and the number of effective parameters (pD), and B) the number of effective replicates. Letters C, D, and E correspond to shape parameters of 24.52, 24.47, and 22.50, respectively. Right panel: posterior mean of the spatial random effect of Bayesian CAR model for each shape parameter defined above.

The occurrence probability of track networks of boreal woodland caribou increased with the proportion of lichen woodland and water bodies in a cell, but decreased with the portion of deciduous stands and disturbances caused by fire and logging (Fig. 1.3). The effect of logging was consistently more negative than that of burning. No significant selection pattern was found for bare lands dominated by terrestrial lichens or for wetlands (Fig. 1.3). The occurrence probability of track networks tended to increase with elevation, but

elevation also showed a greater sensitivity to specification of the shape parameter (Appendix 1.2). The distribution of spatial random effects among Bayesian models revealed strong spatial patterns at multiple scales (Figs 1.4 and 1.5). At coarse scales, favourable winter areas for boreal woodland caribou increased from northeast to west. At intermediate scales, two suitable subregions emerged in the south and northwest parts of the study area. Within these subregions, finer-scale local variation was evident. Although CAR and Matérn models roughly had the same number of effective parameters, the Matérn model allowed describing a latent spatial structure at finer scale, likely because of the flexibility of the Matérn correlation function and because data are on a regular lattice.
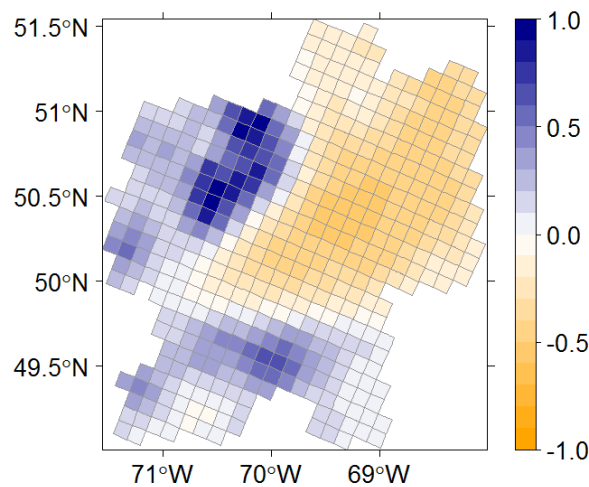
Figure 1.5. Posterior mean of the spatial random effect for hierarchical spatial model with Matérn correlation function.

Overall, CAR and Matérn models improved predictive power by 10% and the percentage of explained deviance by 14% compared with nonspatial logistic model (Fig. 1.6). Uncertainty of the estimates, however, is 5–20% larger for the Bayesian than for the nonspatial logistic model (Fig. 1.3). As expected, models showing higher uncertainty in parameter estimates had higher prediction errors (Fig. 1.6). In no case, was a parameter estimate significant in a spatial and nonspatial model but of differing sign (Fig. 1.3).
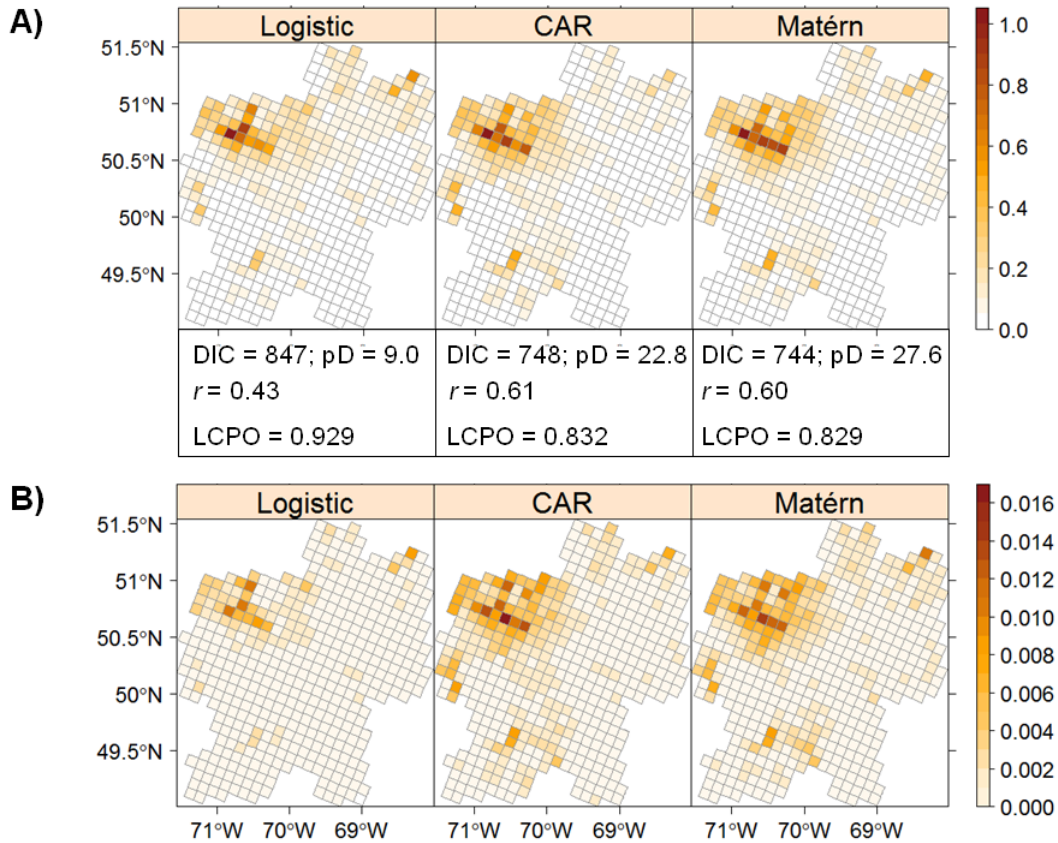
Figure 1.6. A) Mean predicted probability of occurrence of boreal woodland caribou track networks (values have been rescaled to range from 0 to 1); and B) Standard deviation of the predicted probability of occurrence for the statistical methods tested in this study. Below panel A, a summary table shows for each statistical method: 1) Deviance information criteria (DIC); 2) the effective number of parameters (pD); 3) the correlation coefficient between observed and predicted values (r); 4) the log-score statistic ($\overline{\text{LCPO}}$) measuring the predictive power of each model through cross-validation (the lower, the better; see text for further description).

Discussion

Making reliable inferences and robust predictions from the analysis of spatial data is central to many pressing issues in ecology and evolution. Hierarchical spatial models are now routinely used to analyse spatially autocorrelated data as they offer convenient properties such as a flexibility regarding the probability distribution of the response variable, together with their ability to evaluate simultaneously the contributions of fixed predictors and spatial random effects to the likelihood. This last property ensures that variability is properly

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attached to predictions (Gelfand *et al.* 2006) and, if needed, allows predictions to be made at unsampled locations, thereby accommodating gaps in sampling and irregular sampling intensity. In this study, we evaluated a relatively new statistical methodology for estimating hierarchical spatial models, which uses INLA (Rue, Martino & Chopin 2009) as an alternative to MCMC simulations. With this novel numerical inference approach, MCMC sampling becomes redundant as the posterior marginal distributions are accurately approximated in a fully automated fashion (Held, Schrödle & Rue 2010).

Several remarks regarding INLA can be drawn from our study. First, the results of CAR model that were obtained with INLA were so accurate that no tangible difference in model outcomes could be detected with MCMC. This confirms previous comparative results obtained for a wide range of Gaussian latent models (Rue, Martino & Chopin 2009). Second, the processing time for fitting hierarchical spatial models was very rapid, which ultimately allowed us to perform cross-validation tests and sensitivity analyses on priors within a reasonable amount of time. Such a gain in processing time with INLA opens new perspectives in modelling spatial data under the Bayesian framework, as it alleviates one of the most important bottlenecks associated with MCMC. Third, the use of INLA with the R interface greatly facilitates implementation of Bayesian hierarchical spatial models. A strong expertise in programming is thus no longer an obstacle to fitting these models. Fourth, an increasing variety of hierarchical spatial models are now available for end-users (e.g. spatial GLMM, geographic weighted regression, thin-plate splines, among others), which ultimately broadens the range of tools available to ecologists. These models, together with the models presented in this study, allow a wider range of questions to be addressed in ecology and evolution. As with any statistical procedure, INLA also has limitations: precision of approximations becomes less accurate as the number of hyperparameters to be estimated increases above 6; occupancy models containing an observational process to cope with imperfect detection (MacKenzie *et al.* 2002) are not yet implemented in INLA and will require further developments. Site-occupancy models developed for spatially correlated observations in an active area of research (Aing *et al.* 2011); although INLA greatly reduces the processing time relative to MCMC on small to moderate-sized data sets, the spatial modelling of large data sets ($N > 10^6$) remains challenging.

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In hierarchical spatial models, the shape parameter of the gamma distribution that was used as a prior for the precision of the spatial model controls the smoothness of the spatial random effect. The degree of smoothness can be viewed as the spatial equivalent of the pooling factor ω (Gelman & Hill 2007), which represents the degree to which the estimates are pooled together rather than estimated separately for each group factor. Our case study emphasized that parameterization of the shape parameter requires special care. The choice of an uninformative prior favours a low degree of smoothing, which in turn can yield a model that is overfitted to the given observations (see Fig. 1.4a). As described by Plummer (2008), this situation typically occurs when the choice of shape parameter is solely based on DIC comparisons, as DIC can underpenalize model complexity in this class of models. In contrast, highly informative priors increase the degree of spatial smoothing to such a point that the full model becomes equivalent to a nonspatial one (see Fig. 1.4a, b). Up to now, there is no Bayesian equivalent to AICc (see Burnham & Anderson 2002). Hence, we recommend that, based on information theory, the value of the shape parameter be defined so that the ratio between sample size and the number of effective parameters be >20. This stopping rule maintains a balance between information contained in the data and the number of effective parameters (Rue, Martino & Chopin 2009). Sensitivity analyses allow such thresholds to be identified and should be an integral part of any modelling exercise with hierarchical models. Additional work is needed to define Bayesian comparative criteria sensitive to small numbers of equivalent replicates.

Our results on landscape selection patterns largely support previous findings that show boreal woodland caribou avoid regeneration areas following recent disturbance (Vors *et al.* 2007; Courbin *et al.* 2009) and deciduous stands (Courbin *et al.* 2009), which likely mimics a behavioural response to increasing predation risk (Wittmer *et al.* 2007). For example, deciduous stands and regenerating areas are used by moose (Alces alces L.), and increasing moose abundance often translates into higher risk of predation by wolves (Seip 1992; Wittmer *et al.* 2007). The positive selection of water bodies presumably reflects a similar strategy as, on one hand, these large ice-covered open areas improve the ability to detect predators and, on the other hand, surrounding forests enhance the ability to escape from

predators (Mysterud & Ostbye 1999). We found a strong positive selection for lichen woodland that confirms the importance of this habitat in providing arboreal and terrestrial lichens, two major components of boreal caribou winter diet (Johnson, Parker & Heard 2001). Our results also show that, in addition to removing RSA, the inclusion of a spatial random effect yields strong latent spatial patterns at multiple scales that were not explained by environmental covariates. We argue that these latent spatial patterns offer opportunities for researchers to investigate and make further ecological hypotheses about the underlying processes that generated these patterns. For instance, the scale and distribution of spatial random effects could be used as a surrogate in inferring processes from spatial patterns (McIntire & Fajardo 2009). These effects might also be indicative of important missing covariates and further serve sampling strategies by prioritizing locations where data acquisition seems to be the most urgent.

References

Aing, C., Halls, S., Oken, K., Dobrow, R., & Fieberg, J. (2011) A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated, sites. *Journal of Applied Ecology,* **48,** 1508-1517.

Beale, C. M., Lennon, J. J., Yearsley, J. M., Brewer, M. J. & Elston, D. A. (2010) Regression analysis of spatial data. *Ecology Letters,* **13,** 246-264.

Banerjee, S., Carlin, B. P. & Gelfand, A. (2003) *Hierarchical modeling and analysis for spatial data*. Chapman and Hall, Boca Raton, Florida, USA.

Besag, J., York, J. & Mollié, A. (1991) Bayesian image restoration, with two applications in spatial statistics. *Annals of the Institute of Statistical Mathematics*, **43**, 1-20.

Bolker, B. M. (2008) *Ecological models and data in R*. Princeton University Press, Princeton, New Jersey, USA.

Bomhard, B., Richardson, D. M., Donaldson, J. S., Hughes, G. O., Midgley, G. F., Raimondo, D. C., Rebelo, A. G., Rouget, M. & Thuiller, W. (2005) Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Global Change Biology,* **11,** 1452-1468.

Cabeza, M., Araújo, M. B., Wilson, R. J., Thomas, C. D., Cowley, M. J. R. & Moilanen, A. (2004) Combining probabilities of occurrence with spatial reserve design. *Journal of Applied Ecology,* **41,** 252-262.

Courbin, N., Fortin, D., Dussault, C. & Courtois, R. (2009) Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landscape Ecology,* **24,** 1375-1388.

Courtois, R., Gingras, A., Dussault, C., Breton, L. & Ouellet, J. P. (2003) An aerial survey technique for the forest-dwelling ecotype of Woodland Caribou, *Rangifer tarandus caribou. Canadian Field-Naturalist,* **117,** 546-554.

Dormann, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kuhn, I., Ohlemuller, R., Peres-Neto, P. R., Reineking, B., Schroder, B., Schurr, F. M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography,* **30,** 609-628.

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.

Fortin, D., Courtois, R., Etcheverry, P., Dussault, C. & Gingras, A. (2008) Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. *Journal of Applied Ecology,* **45,** 1392-1400.

Gelfand, A. E., Silander, J. A., Wu, S. S., Latimer, A., Lewis, P. O., Rebelo, A. G. & Holder, M. (2006) Explaining Species Distribution Patterns through Hierarchical Modeling. *Bayesian Analysis,* **1,** 41-91.

Gelman, A., & Hill, J. (2007) *Data analysis using regression and multilevel/hierarchical models.* Cambridge University Press, New York, New York, USA.

Haas, S. E., Hooten, M. B., Rizzo, D. M., & Meentemeyer, R.K. 2011. Forest species diversity reduces disease risk in a generalist plant pathogen invasion. *Ecology Letter*s, **14**, 1108-1116.

Held, L., Schrödle, B. & Rue, H. (2010) *Posterior and cross-validatory predictive checks: a comparison of MCMC and INLA in Statistical modelling and regression structures - Festschrift in honour of Ludwig Fahrmeir*. Springer Verlag, Berlin, Germany.

Hilborn, R. & Mangel, M. (1997) *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.

Johnson, C., Parker, K. & Heard, D. (2001) Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia,* **127,** 590-602.

Latimer, A. M., Wu, S. S., Gelfand, A. E. & Silander, J. A. (2006) Building statistical models to analyze species distributions. *Ecological Applications,* **16,** 33-50.

Legendre, P. (1993) Spatial autocorrelation - trouble or new paradigm? *Ecology,* **74,** 1659-1673.

Lindgren, F., Lindstrøm J. & Rue, H. (2011) An explicit link between Gaussian fields and Gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society Series B-Statistical Methodology,* **73**, 423-498.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A. & Langtimm, C. A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

McIntire, E. J. B. & Fajardo, A. (2009) Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology,* **90,** 46-56.

McKenney, D. W., Pedlar, J. H., Papadopol, P. & Hutchinson, M. F. (2006) The development of 1901-2000 historical monthly climate models for Canada and the United States. *Agricultural and Forest Meteorology,* **138,** 69-81.

Minasny, B. & McBratney, A. B. (2005) The Matérn function as a general model for soil variograms. *Geoderma*, **128**, 192-207.

Mysterud, A. & Ostbye, E. (1999) Cover as a habitat element for temperate ungulates: Effects on habitat selection and demography. *Wildlife Society Bulletin,* **27,** 385-394.

Plummer, M. (2008) Penalized loss functions for Bayesian model comparison. *Biostatistics*, **9**, 523-539.

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rue, H. and Held, L. (2005) *Gaussian Markov random fields: Theory and applications*. Volume 104 of Monographs on Statistics and Applied Probability. Chapman and Hall, London.

Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B-Statistical Methodology,* **71,** 319-392.

Seip, D. R. (1992) Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology,* **70,** 1494-1503.

Thogmartin, W. E., Sauer, J. R. & Knutson, M. G. (2004) A hierarchical spatial model of avian abundance with application to cerulean warblers. *Ecological Applications,* **14,** 1766-1779.

Thuiller, W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology,* **9,** 1353-1362.

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,** 1249-1256.

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,** 568-579.

Zuur, A. F., Ieno**,** E.N., Walker**,** N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R.* Springer Science, New York, USA.

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Appendices

Appendix 1.1: R-code for running with INLA all hierarchical models presented in the paper.

Appendix 1.2: Sensitivity analyses of the shape parameter on coefficients of regression

Appendix 1.1. R-code for running all hierarchical models presented in the paper.

```
####################
# 1. Load the Data #
####################
# replace your_path by the path where the data have been saved
datacaribou <-read.table("your_path/data_caribou.txt", sep='', header=TRUE)
str(datacaribou)


################################################
# 2. Non-spatial logistic model fitted with INLA #
################################################
require(INLA)
formula_logistic = y ~ wildfire + logging + lichwood + openlich + deciduous +
water +
                        wetland + meanelev
model_logistic = inla(formula = formula_logistic, data = datacaribou,
                        family ="binomial",
                        Ntrials = Ntrials,
                        control.compute = list(dic = TRUE, mlik = FALSE,
                        cpo = FALSE),
                        control.fixed = list(prec.intercept = 0.001),
                        verbose = F)
summary(model_logistic)


###########################################
# 3. Bayesian CAR model fitted with INLA #
###########################################
require(INLA)
hyperpar_CAR = list(initial = -1, param = c(24.47,0.001))
formula_CAR = y ~ wildfire + logging + lichwood + openlich + deciduous + water +
                  wetland + meanelev +
                  f(node_CAR, model = "besag", graph.file =
                    "your_path/graph_8neighbors.txt",
                  hyper = list(theta = hyperpar_CAR))
model_CAR = inla(formula = formula_CAR, data = datacaribou, family ="binomial",
                        Ntrials = Ntrials,
                        control.compute = list(dic = TRUE, mlik = FALSE, cpo =
                        FALSE),
                        control.fixed = list(prec.intercept = 0.001),
                        verbose = F)
summary(model_CAR)


##############################################
# 4. Bayesian Matérn model fitted with INLA #
##############################################
require(INLA)
nrow.larger = 51
ncol.larger = 44
log.range = list(initial = log(5), fixed=TRUE)
hyperpar_matern = list(initial = -3, param=c(23.37,0.001))
formula_matern = y ~ wildfire + logging + lichwood + openlich + deciduous +
                        water + wetland + meanelev +
                        f(node_matern, model = "matern2d", nrow = nrow.larger,
                          ncol = ncol.larger, hyper = list(range = log.range, prec
                          = hyperpar_matern))
model_matern = inla.cpo(formula = formula_matern, data = datacaribou, family =
                          "binomial", Ntrials = Ntrials,
                          control.compute = list(dic = TRUE, mlik = TRUE, cpo =
                          FALSE),
                          control.fixed = list(prec.intercept = 0.001))
summary(model_matern)
```

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Appendix 1.2. Effect of the shape parameter on coefficients of regression (± 95% CI). White dot represents the posterior mean of the non-spatial logistic model and black dots represent the posterior mean of the CAR model.
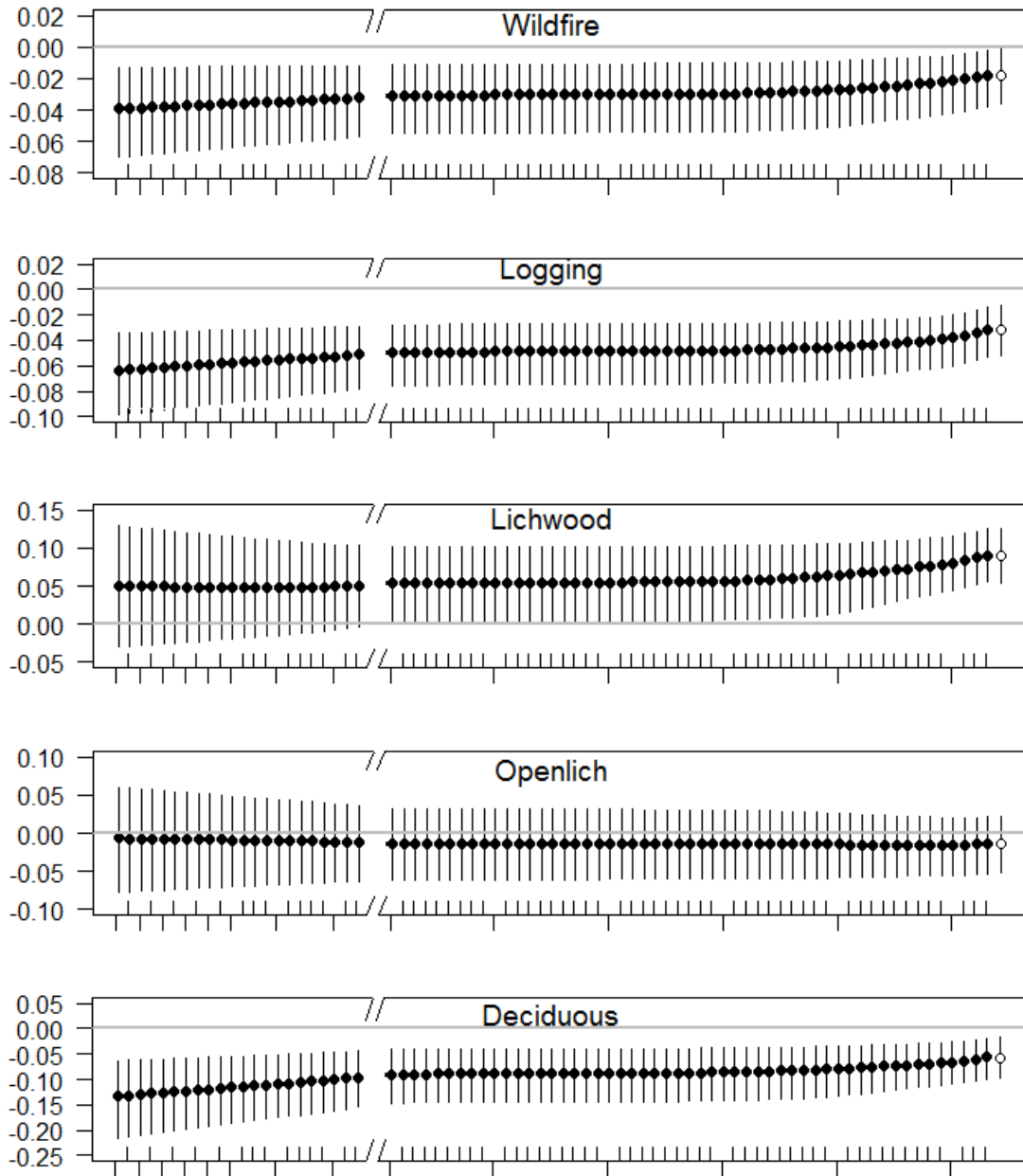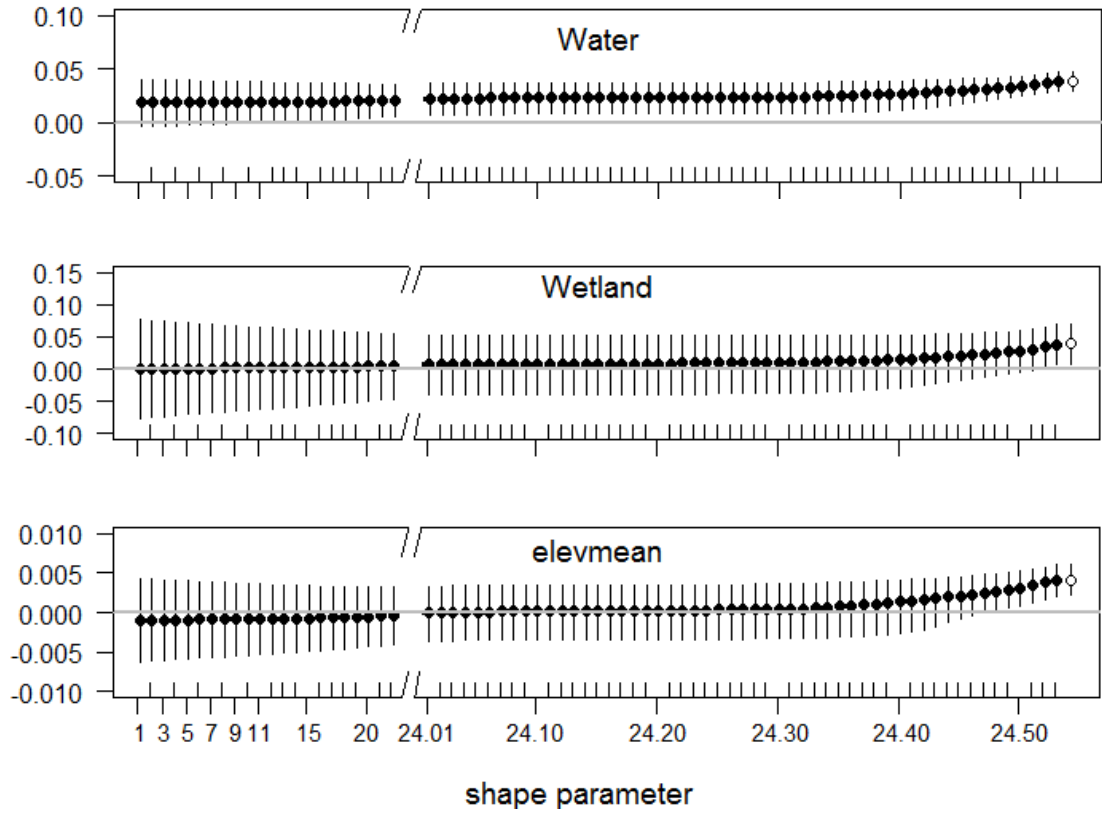
CHAPITRE 2:

EXPLAINING GEOGRAPHIC GRADIENTS IN WINTER SELECTION OF LANDSCAPES BY BOREAL CARIBOU WITH IMPLICATIONS UNDER GLOBAL CHANGES IN EASTERN CANADA

JULIEN BEGUIN, ELIOT J.B. MCINTIRE, DANIEL FORTIN, STEVEN G. CUMMING, FRÉDÉRIC RAULIER, PIERRE RACINE & CLAUDE DUSSAULT

Résumé

Plusieurs espèces animales répondent selon des gradients longitudinaux et latitudinaux aux composantes biotiques ou abiotiques de leur habitat. Comprendre le(s) mécanisme(s) biologique(s) à l'origine de ces patrons spatiaux peut être décisif pour développer des mesures de conservation appropriées au maintien ou au rétablissement d'espèces menacées d'extinction. Toutefois, peu d'études ont identifié le ou les processus écologique(s) qui sont à l'origine de l'existence de gradient(s) géographique(s) dans la sélection d'habitat. Nous avons utilisé un jeu de données spatiales couvrant une grande amplitude géographique pour tester trois hypothèses qui pourraient expliquer la présence de gradients géographiques dans la sélection de l'habitat par le caribou forestier (*Rangifer tarandus caribou*): 1) l'hypothèse d'une sélection orientée de façon prédominante par le climat, qui postule que les gradients géographiques sont la conséquence de gradients climatiques sous-jacents; 2) l'hypothèse d'une sélection de l'habitat orientée de façon prédominante par la distance aux routes, qui propose que les individus ajustent leur sélection de certaines catégories d'habitat en fonction de la proximité par rapport aux routes; 3) l'hypothèse d'une sélection découlant d'un effet additif du climat et de la proximité de routes. Nos données supportaient mieux la deuxième hypothèse d'une sélection orientée par la distance aux routes, plutôt que la première hypothèse climatique. En conséquent, l'empreinte laissée dans les paysages par les activités humaines conditionne en grande partie la distribution spatiale du caribou forestier et cette prédominance devrait perdurer aussi longtemps que les conditions climatiques futures ne changent pas suffisamment par rapport aux conditions actuelles. Nos résulats montrent également que l'évitement par le caribou forestier des aires de coupes forestières était deux fois plus marqué que l'évitement des brulis récents. Limiter l'étalement du réseau routier et prendre en compte l'effet inégal des coupes par rapport aux brulis devraient donc faire partie intégrante du plan de gestion de l'habitat du caribou forestier et des mesures de conservation à l'intérieur de son aire de répartition actuelle. Finalement, nous avons identifié d'importants patrons spatiaux latents qui fournissent un éclairage intéressant pour générer des hypothèses alternatives sur le type de processus impliqué dans la distribution actuelle du caribou forestier dans l'est du Canada.

Summary

Many animal species exhibit broad-scale latitudinal or longitudinal gradients in their response to biotic and abiotic components of their habitat. Although knowing the underlying mechanism of these patterns can be critical to the development of sound measures for the preservation or recovery of endangered species, few studies have yet identified which processes drive the existence of geographical gradients in habitat selection. Using extensive spatial data of broad latitudinal and longitudinal extent, we tested three hypotheses that could explain the presence of geographical gradients in landscape selection of the endangered boreal woodland caribou (*Rangifer tarandus caribou*) during winter in eastern Canadian boreal forests: 1) climate-driven selection, which postulates that geographic gradients are surrogates for climatic gradients; 2) road-mediated selection, which proposes that boreal caribou adjust their selection for certain habitat classes as a function of proximity to roads; and 3) an additive effect of both roads and climate. Our data strongly supported road-driven selection over climate influences. Thus, direct human alteration of landscapes influences boreal caribou distribution and should likely remain so until the climate changes sufficiently from present conditions. Boreal caribou avoided logged areas two-fold more strongly than burnt areas. Limiting the spread of road networks and accounting for the uneven impact of logging compared to wildfire should therefore be integral parts of any habitat management plan and conservation measures within the range of the endangered boreal caribou. The use of hierarchical spatial models allowed us to explore the distribution of spatially-structured errors in our models, which in turn provided valuable insights for generating alternative hypotheses about processes responsible for boreal caribou distribution.

Introduction

The actual magnitude of global change that can be attributed to climate change and human-induced alterations of landscapes raises concerns about the adaptive abilities of many species to persist in this fast-changing world (Thuiller 2007). This view is supported by high current extinction rates for amphibians, birds, and mammals that are comparable to the rates prevailing during the last Big Five mass-extinction events, which have occurred over the past 443 million years (Barnosky *et al.* 2011). Global warming and increasing anthropogenic disturbance are thought to be the two most important causes of current global change and the main causes of declines in biodiversity (Pereira *et al.* 2010)**.** While both of these threats are anthropogenic (IPCC 2007), the ways of addressing species losses that are attributable to these two alternatives are quite different. Knowing which factor is most important in particular instances is vital if we are interested in putting into practice sound conservation measures for endangered species.

In free-ranging animals, habitat selection is a fundamental behavioural process that structures their spatial distribution and influences population dynamics (Morris 2003). Fortin *et al.* (2008) recently showed that the strength of selection (i.e., the relative probability of occurrence) for certain habitats varies along broad geographic gradients such as latitude and longitude, suggesting that large-scale processes may modulate the way in which animals respond locally to their environment. This result adds to previous findings that many mammal species exhibit broad-scale gradients in their responses to the environment, for example, through increasing body mass with latitude as predicted by Bergmann's rule (Ashton *et al.* 2000; Herfindal *et al.* 2006) or through changes in the strength of density-dependence relationships along latitude and longitude (Post 2005). Change in habitat selection patterns along broad geographical gradients has both theoretical and practical implications. On one hand, it leads one to ask which ecological processes are responsible for this pattern; on the other hand, it stresses the need for management and conservation strategies that account for regional specificities in species responses to their environment. Despite their relevance in the context of global change, few attempts have been made to clarify possible causes of latitudinal and longitudinal gradients in habitat selection by moving organisms (Oliver *et al.* 2009). Latitude and longitude could be proxy

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variables for key drivers of global change such as climate conditions (e.g., temperature and precipitation) or human-induced alterations of landscapes. Thus, understanding the biological basis for such broad geographical trends would allow us to effectively determine species management priorities.

We considered forest-dwelling or boreal woodland caribou (*Rangifer tarandus caribou*), hereafter boreal caribou, as a case study because it is a wide-ranging threatened ecotype (COSEWIC 2002) for which broad geographical gradients in landscape selection have been previously reported (Fortin *et al.* 2008). Our study focused on the Canadian eastern boreal forest within the southern part of the continuous range of boreal caribou. The sensitivity of boreal caribou to human-induced disturbances (e.g., logging (Courtois *et al.* 2008); roads (Wasser *et al.* 2011); petroleum and natural-gas infrastructures (Dyer *et al.* 2001)) is well documented throughout its distributional range in Canada. Further, these disturbances are thought to be the main causes of range recession in eastern North America (Schaefer 2003; Vors *et al.* 2007; Environment Canada 2008; Festa-Bianchet *et al.* 2011). Consequently, current conservation efforts are mainly oriented towards lowering human pressure on boreal landscapes (Environment Canada 2008). Contrary to the situation in the western provinces of Canada where several boreal caribou populations are geographically isolated and the rate of anthropogenic disturbances is high within population ranges (Environment Canada 2012), the eastern boreal forest of Québec still contains large tracts of intact boreal forest, especially further north. In the context of lowering the human footprint, it is possible that climate plays an important role in the spatial distribution of boreal caribou. However, the role of climate in determining the large-scale distribution of, and landscape selection by boreal caribou has not been established. Climate can influence caribou through its direct and indirect effects on snow conditions, on forage accessibility and abundance, on levels of insect harassment, and on competition and predator-prey interactions (Vors & Boyce 2009). Climate is known to influence the seasonal spatial distribution of migratory tundra caribou (*R. t. caribou*) (Sharma *et al.* 2009). As the winter ranges of these two neighbouring ecotypes partially overlap in eastern Canada (Boulet *et al.* 2007), boreal caribou also may respond to climatic gradients. The relative effects of climate and disturbance, or their additive effects on boreal caribou distribution have yet to be

quantified. Disentangling the underlying processes from observed spatial patterns (Fortin & Dale 2005; McIntire & Fajardo 2009) can be challenging when spatial patterns originate from several processes that act in concert or when multiple causal processes have confounding spatial signatures at a given observational scale (Levin 1992). These issues are recurrent in macroecology and global change biology where, for example, the spatial distribution of climatic variables at low resolution often correlates with gradients in landscape alterations (Thuiller *et al.* 2004), making it unclear if climate alone, land-use patterns alone, or their synergistic effects drive species distributions at a broad spatial scale. Fortin *et al.* (2008) reported residual spatial and geographic gradients, but it was not clear whether these gradients resulted from broad-scale effects of roads or they emerged from spatial variation in climate.

Our study objectives were thus threefold. First, we tested three alternative *a priori* hypotheses regarding the possible causes of geographic gradients on caribou habitat selection: climate-driven selection, road-driven selection, and selection that is driven by an additive effect of climate and roads. The hypothesis of climate-driven selection assumes that previously known geographic gradients are a surrogate for climatic gradients in temperature and precipitation and that selection of certain habitats varies along climatic zones. The road-driven selection hypothesis reflects a trade-off between security and nutrition in which the boreal caribou adjusts its selection of certain habitat classes as a function of distance to roads (Wasser *et al.* 2011; Dussault *et al.* 2012). The additive hypothesis considers that both factors act in concert. Second, we offer a comparative evaluation of the marginal impacts of logging and wildfire on boreal caribou spatial distribution to inform future conservation and ecosystem-based management strategies in the eastern boreal forest. Last, in exploring spatially structured errors in our models, we provide further testable hypotheses regarding alternative ecological processes involved in the broad-scale spatial distribution of boreal caribou.

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Materials and Methods

Study area

The study region (~237 500 km^2) was located in the coniferous boreal forest of eastern Canada (Fig. 2.1), within the southern range of forest-dwelling caribou in the Province of Québec.
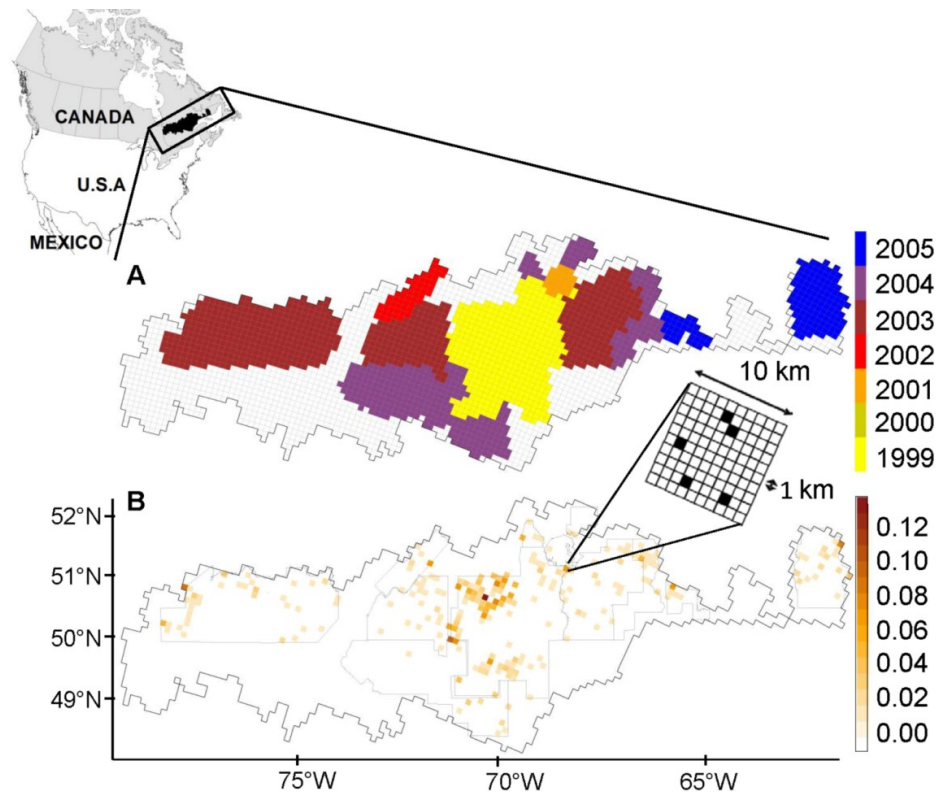
Figure 2.1. Study area showing A) the spatio-temporal design of areal-surveyed blocks for the presence/absence of boreal caribou track networks; B) the proportion of intensive caribou track networks in each 100 km^2 cell. Limits of inventory blocks are depicted by cells of different colours in (A) and by light grey contour lines in (B). Uncoloured cells in (A) are located outside inventory blocks and are left unmonitored for the presence/absence of caribou track. White cells located within inventory blocks in (B) are monitored but correspond to the absence of caribou track.

The study area covered a wide geographic extent, ranging from 1300 km in longitude to 450 km in latitude. The area exhibited a high degree of variation in mean annual temperature (-4.0^{o}C to 2.3^{o}C), which is fairly representative of the mean annual temperatures observed across the natural range of boreal caribou (-7.1^{o}C to 3.9^{o}C,

Environment Canada 2011). The percentage of the landscape that has been affected by anthropogenic disturbance in our study region (from 12 to 51 %) was comparable to that observed in many regions of Ontario (1 - 36 %) and Manitoba (3 - 26 %), but much lower than what has been witnessed in the western provinces of Alberta (21 - 95 %) and British Columbia (57 - 86 %) (Environment Canada 2012; see Appendix G, Table G.1). The area also exhibited high variability in road density from north to south (0 to 5.1 km/km^2; Table 2.1). Vegetation was dominated by coniferous stands in which black spruce (*Picea mariana* (Miller) BSP), balsam fir (*Abies balsamea* (L.) Miller), and jack pine (*Pinus banksiana* Lambert) are the most frequently encountered canopy species (Table 2.1). White or paper birch (*Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michaux) are found as companion species or in pure stands following recent disturbance. Open water bodies, wetlands, and bare land covered 11%, 10%, and 7% of the study area, respectively. Elevations ranged from 50 to 1000 m a.s.l., with plains and gentle hills (100-450 m) west of longitude 75°, and more rugged hills (300-1000 m) in the east. Wildfire and logging activities were the main disturbances throughout the region. The fire regime varies along a west-east gradient, with a shorter mean fire return interval in the west (Bergeron *et al.* 2004; Bouchard *et al.* 2008). Extensive logging started in the early 1970's in the southern part of the region and has since extended northwards, together with the road network. Contrary to barren-ground migratory caribou, the boreal caribou is sedentary and its spatial distribution ranges within the geographical limits of the Canadian boreal forest (Festa-Bianchet *et al.* 2011), from the eastern province of Newfoundland to the western province of British Columbia. In winter, boreal caribou live in small scattered and mobile groups of a few individuals. Caribou rely essentially on lichen in winter across its distribution range (Courtois *et al.* 2008; Thomas *et al.* 2011), but lichen is not limiting in some landscapes in Québec (Courtois *et al.* 2008). Boreal caribou has "vulnerable species" status in Québec.

Caribou and environmental data

Our observational units were presences and absences of intensive caribou snow-track networks that had been observed during the winter season. A caribou snow-track network (hereinafter called caribou tracks) delineates an area that is used briefly and intensively in winter by a small group of caribou for foraging or shelter. These caribou tracks are thus

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closely related to the biological needs of boreal caribou in winter, a critical season for temperate ungulates (see Fortin *et al.* (2008) and references therein). Caribou tracks were sampled from intensive fixed-wing aerial surveys, which were backed by helicopter spot-checks, conducted in the winters of 1999 through 2005 (for details, see Fortin *et al.* (2008) and Courtois *et al.* (2003)). The surveys were conducted along transects within 11 spatial-temporal survey blocks (Fig. 2.1). The probability of caribou track detection given presence was high (≥ 90 %), due to strong contrasts between caribou track and adjacent undisturbed snow surfaces (Courtois *et al.* 2003). Given the high detectability of caribou tracks and the intensity of sampling efforts, false positives and false negatives were ignored in this analysis.

We related the probability of occurrence of winter caribou tracks to environmental conditions using 18 covariates belonging to four different classes of variables: habitats, disturbances, roads, and climate (Table 2.1). These environmental covariates were obtained from up-to-date digital forest inventories (MRNFQ 2003) and interpolated monthly climate data (McKenney *et al.* 2006). Forest inventory data allowed us to distinguish between forested and non-forested polygons. Forested polygons were classified according to species composition, density, and height (Table 2.1). Non-forested polygons distinguished various land-types such as disturbances, wetlands and water bodies. The classification of forested and non-forested variables based on information provided in forest inventory mapsheets is explained in Appendix 2.1. For testing the role of climate surfaces in explaining geographical gradients in habitat selection, we used 30-year averages of mean temperature and precipitation calibrated from 1970 to 1999 (hereafter called normals). The rationale for this choice is as follows: 1) these variables are the main climatic inputs for global climate models (GCMs), making their use potentially relevant to assessing future direct impacts of climate change, if any, on boreal caribou distribution; 2) prediction errors that are associated with these primary variables are low (McKenney *et al.* 2006). In contrast, the prediction error of snow depth data in our study was high, so that variable was not included in our models. 3) Temperature and precipitation data serve as main inputs for calculating derived climatic indices, making correlations between climate indices and these primary variables very likely.

Table 2.1. Environmental variables used as predictors in our study. Minimum, mean and maximum values of each explanatory variable, at the scale of 100 km2 grid cells, are presented for the entire region. Only variables that are shown in bold type were retained in the analysis of model comparisons (i.e., "road density" was discarded because of its high correlation with "logging," i.e., r = 0.85).

Group	Variables	Description	Min.	Mea	Max.
Habitat	black spruce - jack pine (km^2) §	coniferous stands with basal area dominated by black spruce and jack pine, or the converse	0	3.2	41.2
	black spruce (km^2) §	coniferous stands with basal area dominated by black spruce	0	23.0	74.1
	black spruce- balsam fir (km^2) §	coniferous stands with basal area dominated by black spruce and balsam fir, or the converse	0	12.6	73.2
	balsam fir (km^2) §	coniferous stands with basal area dominated by balsam fir	0	1.5	29.5
	jack pine (km^2) §	coniferous stands with basal area dominated by jack pine	0	0.8	26.9
	mixed coniferous (km^2) §	mixed stands with basal area dominated by coniferous species	0	2.5	30.8
	lichen woodland (km^2)	coniferous stands of low density with abundant ground lichen	0	1.6	29.6
	deciduous (km^2)	stands with basal area dominated by deciduous species (mainly birches and aspens)	0	1.4	39.0
	mixed deciduous (km^2)	mixed stands with basal area dominated by deciduous species and followed by coniferous species	0	2.6	52.2
	lichen heaths (km^2)	open dry sites with abundant ground lichen	0	2.9	42.1
	water bodies (km^2)	lakes and rivers	0.1	11.2	93.1
	wetlands (km^2)	bogs and fens	0	10.0	83.1
Road	road density (km/km^2)	total road length by area unit (including all types of roads)	0	0.5	5.1
	mean distance to road (km)	average distance to all types of roads	0	10.3	105.5
Disturbance	logging (km^2)	areas recently logged and with actual maximum tree height < 7	0	13.5	82.5
	wildfire (km^2)	areas recently burned and with actual maximum tree height < 7	0	5.5	80.2
Climate	Normal annual mean temperature (˚C) ¶	interpolated mean annual temperature (1970-1999)	-4.0	-0.8	2.3
	Normal annual total precipitation (mm) ¶	interpolated total annual precipitation (1970-1999)	740.9	976.1	1214.8

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Notes of Table 2.1:

§ To avoid multi-collinearity, all types of coniferous stands were reduced using principal component analysis: see appendix 2.2.

¶ We also used winter normals of temperature and precipitation but no difference was observed, so we only retained annual variables

Seasonal and annual climatic variables were highly correlated ($r > 0.8$) and we found no difference in the results when climate variables were measured annually or over winter months. Therefore, we only retained 30-year annual normals, which were more likely to interact with vegetation attributes than just the winter climatic variables. Given the size of the data set (> 5 GB), all spatial data were processed using the open-source spatial database system PostGis (http://postgis.refractions.net/). Spatial resolution of covariates varied from 8 ha for forest inventory attributes to ~100 km^2 for climate data. All attributes were calculated as total areas or averages over a common 100 km^2 grid, which was defined by the climate data (see Table 2.1). Hereafter, each elementary unit of this grid is referred to as a "cell" (see Fig. 2.1). Each covariate was then normalised by subtracting the mean and dividing by the standard deviation. We calculated 14 land cover covariates from the forest inventory data as proportional areas of various types of forested and non-forested habitats. Of these, six variables referred to various types of coniferous forest (Table 2.1). To avoid multicollinearity, we performed principal component analysis (PCA) with a covariance matrix based on these 6 variables and retained sample scores of the two most significant orthogonal axes as model covariates (see Table S1 in Appendix 2.2). Variance inflation factors in the reduced data set were < 3 for all covariates, indicating that multicollinearity amongst the predictors was not an issue (Zuur *et al.* 2009). Caribou presence/absence data were calculated for a 1-km^2 resolution sub-grid (see Fig. 2.1). This resolution was roughly twice the mean of caribou track area (0.53 km^2, SE $\pm$ 0.06 km^2: see [32]) and well below the size of the winter home range, which typically varies from about 100 to 700 km^2 (Faille *et al.* 2010; Bastille-Rousseau *et al.* 2012).

Statistical analyses

We built our candidate models upon alternative *a priori* hypotheses where the presence of geographical gradients in landscape selection was a surrogate for: *i*) an effect of climate, alone or in interaction with covariates (models 5 and 8; Table 2.3); *ii*) an effect of distance to roads, alone or in interaction with covariates (models 4 and 7; Table 2.3); or *iii*) an additive effect of climate and distance to roads with possible interactions with covariates (model 9; Table 2.3). For completeness, we include several neutral models: intercept only, landcover only, geography and land cover only, and geography, landcover and interactions (models 1, 2, 3 and 6, respectively; Table 2.3). All candidate models had the same structure but differed in their design matrix x_i' (Appendix 2.3). Let n_i be the number of 1-km^2 sub-cells within the ith cell, and Y_i is the number of these sub-cells where the presence of caribou track is observed. We assumed Y_i to be a binomial random variable and have modelled the probability p_i of caribou track presence within cells using a logit link function and the following generic generalised linear mixed model (GLMM):

$$Y \sim \text{Binomial}(n_i,\ p_i),$$
$$\text{logit}(p_i) = \boldsymbol{\beta}\ x_i' + \alpha_{k(i)} \qquad\qquad \text{[Equation 1]}$$

where x_i' is the vector of standardised covariates of each candidate model for each cell i; $\boldsymbol{\beta}$ is the vector of parameters associated with environmental covariates to be estimated for each candidate model, where each β_j is assigned a vague prior such as $\beta_j \overset{iid}{\sim} \mathcal{N}(\text{mean} = 0,$ precision $= 0.001$); α_k is a random intercept of the kth inventory block ($k = 1,\ldots, 11$; see Fig. 2.1A) that accounts for a block-specific value for intercept α_k, where $\alpha_k \overset{iid}{\sim} \mathcal{N}(\text{mean} = 0,$ precision $= \tau$) and the hyperparameter τ is assigned a vague prior $\sim$ Gamma(shape $= 1$; scale $= 5e\text{-}05$).

We verified that residual spatial autocorrelation (RSA) did not affect the model selection procedure (see Figure S3 and Appendix 2.4). In addition to model selection and hypothesis tests, we were also interested in making inferences on parameters, especially in comparing the impact of fire *vs* logging on boreal caribou space use. Indeed, disentangling these

effects is of particular concern from a conservation and ecosystem-based management perspective. Inference on model parameters, however, is particularly sensitive to RSA (e.g., increasing type-I error) so we explicitly modelled spatial associations amongst cells by adding a spatial random effect, with a Matérn correlation function, to the simplest and top-ranked model that had been previously selected (Appendix 2.5). The addition of a spatial random effect to Equation 1 also allowed us exploring the spatial structure in model errors which can, in turn, inform us about important ecological processes not accounted for in our models. All models were fit in R v2.14.2 (R Development Core Team 2011), using integrated nested Laplace approximation (INLA) within the R-INLA package (Rue *et al.* 2009), which is freely available at www.r-inla.org.

Results

As expected, distance to roads was positively correlated with latitude, whereas the mean temperature gradient was negatively correlated with latitude. Precipitation was positively correlated with longitude (Table 2.2). Based on non-spatial GLMMs with 100% of the data, the ΔDIC between model 6 (DIC = 1769) and models 2 and 3 (DICs ≥ 1800) was greater than 30 (Table 2.3), indicating that the existence of geographical trends in caribou selection of lichen woodland, logging areas and water bodies better explained the data than did the hypothesis of homogeneous selection of these habitats across the study region. We failed to detect any top-down climatic control on these geographical gradients, as the models with climate variables alone or in interaction with land cover (models 5 and 8; Table 2.3) had less support than did model 6, which contained only geographical gradients (ΔDIC > 30; Table 2.3). In addition, climate variables only marginally explained extra information that was not already explained by land cover and disturbance variables (ΔDIC ≤ 2 between models 5 and 2; Table 2.3).

Table 2.2. Pearson product-moment correlations (r) among values of geographical UTM coordinates of cell centroids (X for longitude and Y for latitude), annual climatic normals of total precipitation and mean temperature, and mean distance to roads (see Table 2.1 for variable descriptions). Values in bold highlight |r| values > 0.5.

	X (km)	Y (km)	Total precipitation (mm)	Mean temperature (°C)	Distance to roads (km)
X (km)	1				
Y (km)	0.24	1			
Total precipitation (mm)	**0.84**	-0.19	1		
Mean temperature (°C)	0.22	**-0.81**	-0.01	1	
Distance to roads (km)	0.26	**0.60**	0.01	**-0.69**	1

Overall, models that included distance to roads, alone or in interactions with other landcover types (models 4, 7, 9), and the model that included interactions between latitude and landcover types (model 6) were the most supported amongst all of the candidate models. Model 6 indicated geographical trends in caribou selection, but we do not discuss it further because of its lack of mechanistic explanation. Model 9, which included interaction terms between climate and landcover types, had lower support than models 4 and 7, both without climatic variables ($\Delta DIC \geq 3$; Table 2.3), which indicates that addition of climate variables did not improve the fit of models 4 and 7. The low contribution of climate, alone or in interaction with land cover, to the model fit is further seen in the low support of models 5 and 8 (Table 2.3). The model with a single effect of the mean distance to road (model 4) and model 7, with an interaction between distance to road and landcover types, were thus the best-supported candidate models. This shows that the large-distance effect of roads, rather than climate, plays an important role in boreal caribou habitat selection and provides an explanation for geographical trends that was observed in habitat selection patterns.

Table 2.3. Model comparisons for the different a priori hypotheses tested in this study. Geographic-driven selection is represented by model IDs 3 and 6, climate-driven selection by model IDs 5 and 8, and selection that is driven by distance to roads is represented by model IDs 4 and 7. Interaction effects between two variables are indicated by a colon (:). The hypothesis of an additive effect of climate and distance to roads is represented by model ID 9. Variable names: pD = the number of effective parameters; REP = the mean number of data point for each effective parameter; and DIC = Deviance Information Criteria. See Table 2.1 for a description of variables.

ID model	Hypothesis	Variables	pD	REP	DIC
4	distance to road (= distroad)	land cover + distroad	20	85	1766
7	distroad x covar	land cover + distroad + distroad:logging + distroad:woodlichen + distroad:water	23	74	1766
6	geog x covar	land cover + X + Y + Y:logging + Y:lichen woodland + Y:water ¶	24	71	1769
9	distroad x covar + climate x covar	land cover + distroad + meanprec + meantemp + meantemp:logging + meantemp: lichen woodland + meantemp:water + distroad: lichen woodland + distroad:logging + distroad:water	28	61	1769
8	climate x covar	land cover + meanprec + meantemp + meantemp: logging + meantemp: lichen woodland + meantemp:water	24	71	1795
3	Geographic (= geog)	X + Y + land cover ¶	21	80	1800
5	climate	land cover + meanprec + meantemp	21	81	1801
2	land cover only	land cover §	19	89	1803
1	intercept only	intercept	9	201	2094

Notes of table 2.3:
§ land cover = intercept + wildfire + logging + lichen woodland + lichen heaths + water + wetlands + coniferous stands PC1 + coniferous stands PC2 + deciduous + mixed deciduous (see Table 2.1 for a definition of variables).
¶ X and Y represent the geographic coordinates of centroids of each 100 km^2 cell.

We could not distinguish, however, whether model 4 or 7 had the better fit (ΔDIC $\leq$ 2; Table 2.3). For inference, we adopted a pragmatic view and retained a spatial version of model 4, as it was the simplest top-ranked model. Boreal caribou positively selected water bodies and areas that were located far from roads, whereas they avoided deciduous stands

and disturbances that had been caused by fire and logging (Table 2.4). Logged areas were avoided twice as strongly as burnt areas, showing that boreal caribou did not respond to these two disturbances in the same manner (Table 2.4). Boreal caribou tended to select positively lichen woodland, but the parameter estimate for this variable also exhibited a greater sensitivity to specification of the spatial random effect (Figure S4 in Appendix 2.5). No selection pattern was detected for coniferous and mixed stands, wetland, or open habitat with lichen ground cover (Table 2.4). Mapping spatial random effects revealed strong latent spatial patterns at multiple scales (Fig. 2.2A). At a coarse scale, favourable areas for boreal caribou are mainly concentrated in a large band that is centred on 70°W longitude and which extends from 48° to 52°N latitude. At an intermediate scale, suitable sub-regions emerged in the northern part of the study area, whereas unfavourable sub-regions appeared mainly in the central and southern parts of the study region. Within these sub-regions, finer-scale local variation was present. This multi-scale spatial pattern showed very low sensitivity to prior specification of the spatial random effect, as it was consistent for a wide range of values for the precision hyperparameter τ. As expected, uncertainty in the spatial random effect increased with increasing distance from the points at which data had been collected (Fig. 2.2B).

Table 2.4. Marginal posterior medians of parameter estimates (with 95% credible intervals) for the spatial version of model 4 (see Table 2.3). Variable are described in Table 2.1.

Variables	2.5%	50%	97.5%
Logging	-1.17	-0.76	-0.39
Wildfire	-0.61	-0.37	-0.14
Coniferous stands (PC 1)	-0.32	-0.06	0.21
Coniferous stands (PC 2)	-0.24	-0.05	0.14
Lichen woodland	-0.03	0.10	0.23
Deciduous	-1.18	-0.70	-0.10
Mixed deciduous	-0.32	0.04	0.34
Lichen heaths	-0.29	-0.13	0.03
Water	0.11	0.30	0.48
Wetlands	-0.25	-0.01	0.23
Mean distance to road	0.07	0.29	0.46
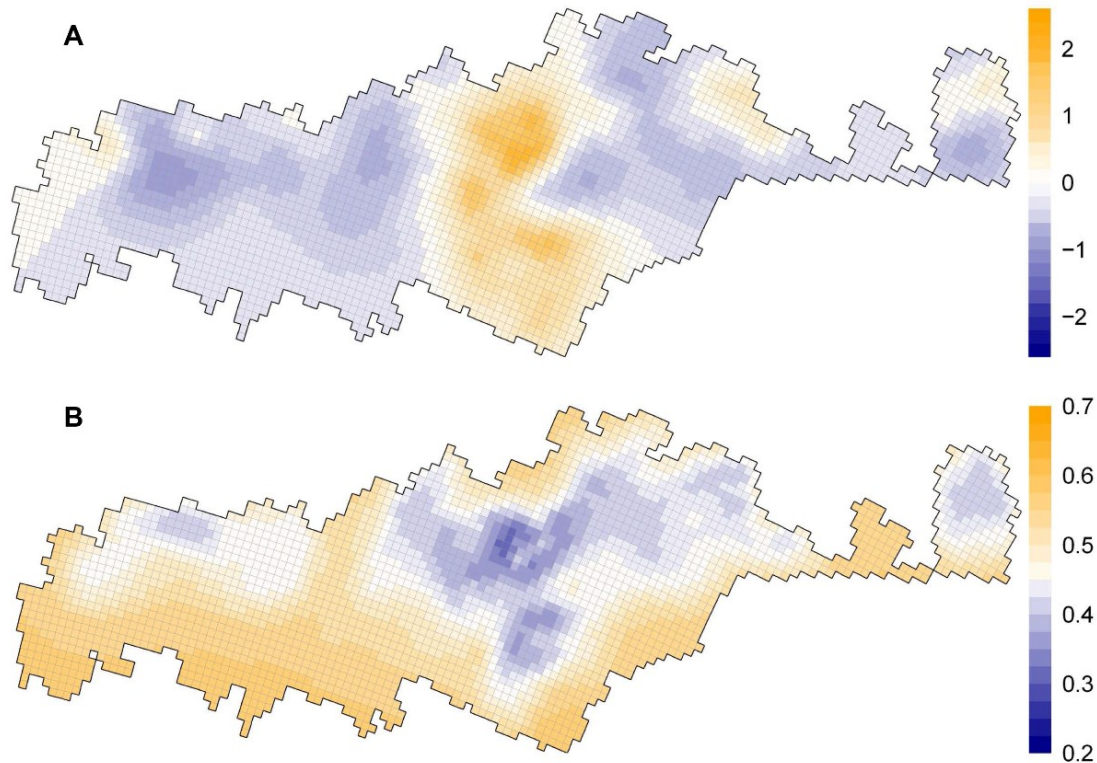
Figure 2.2. Map of the posterior mean (A), and posterior standard deviation (B) of the spatial random effect.

Discussion

We rejected both the hypothesis of climate-driven winter selection of landscapes and the hypothesis of an additive effect of climate and distance to roads. Indeed, temperature and precipitation normals, which are the main inputs that are used in climate change scenarios, did not explain latitudinal trends observed in the winter selection of certain habitat classes by boreal caribou. Moreover, we failed to detect any effect of temperature and precipitation variables alone on the winter distribution of boreal caribou within its southern range, once land cover and disturbance types were taken into account. These results contrast with evidence that temperature and precipitation play an important role in the winter distribution of the largest herd of migratory caribou in Québec (Sharma *et al.* 2009), indicating that both ecotypes may not respond to the same environmental filters. From this difference, it can be anticipated that climate changes - specifically changes in mean temperature and total precipitation - should have more short-term direct impacts in winter on migratory caribou

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than on boreal caribou, at least within its southern range. The mechanisms for the apparent climate sensitivity of the migratory ecotype remain unknown but could be related to summer food limitation (Couturier *et al.* 2010) – a rare or non-existent circumstance for the boreal ecotype. Although snow depth can influence fine-scale habitat selection of boreal caribou (Courbin *et al.* 2009), the lack of precision of snow depth estimates at broad spatial scale prevented us to test reliably for the effect of snow depth on boreal caribou winter distribution and the possible relationship between snow depth and climatic variables. Further studies are needed to document the possible interrelationships amongst temperature, precipitation, snow conditions and the spatial distribution of boreal caribou. It is also important to assess if climate changes affect landscape selection by boreal caribou during the snow-free season and at larger spatial scales than in the present study. Our failure to detect any direct influence of seasonal or annual trends in mean temperature and total precipitation, however, does not imply that climate change will have no indirect effects on boreal caribou during winter. For example, climate change is expected to change the amount and spatial distribution of the area that is burned in the boreal forest of North America (Balshi *et al.* 2009). In turn, burnt areas will influence winter habitat selection, as shown in our study and by several others (Schaefer & Pruitt 1991; Rettie & Messier 2000). A full assessment of indirect effects of climate change on caribou spatial distribution will require further development of a dynamic multivariate simulation model that would explicitly model interdependencies over space and time amongst climate variables, disturbance regimes, vegetation types, and predator-prey interactions.

The hypothesis of road-driven selection was well supported by our data. Our findings were consistent with previous studies showing that the boreal caribou avoids roads (Wasser *et al.* 2011; Fortin *et al.* 2013). We found an equivalent support for both hypotheses of dependence (model 7) and independence (model 4) in the selection of lichen woodland, water bodies, and logging areas with distance to roads. Our failure to discriminate these two alternatives could be related to the spatial resolution of our models, which might be too low for matching the finer spatial scale at which road distance-based selection might occur. MacArthur (1972) hypothesised that in the northern hemisphere, species distributions are more likely to be limited by biotic interactions at the southern margin of their range and by

abiotic factors at the northern edge. In this study, which occurs at the current southern range limits of boreal caribou, roads likely act as a surrogate for higher densities of alternate prey (e.g., moose) and predators (e.g., wolves) – the prevailing hypothesis for the decline of forest-dwelling caribou (e.g., Festa-Bianchet *et al.* 2011). The predominance of human-induced disturbances over climate-induced effects in explaining distributional patterns of boreal caribou is in accordance with expectation. This is also consistent with a broad-scale niche analysis of this ecotype (Environment Canada 2008; section 6.4). Hence, this study reinforces previous recommendations (Schaefer 2003; Vors *et al.* 2007; Environment Canada 2008) that habitat conservation measures for boreal caribou should concentrate on minimising road density and logging areas at the landscape-level but also on reducing broad-scale expansion of road networks into the current ranges of boreal caribou.

The management of boreal forest in the Province of Québec, including coniferous forests that are located within the southern range of boreal caribou, has recently changed paradigms from sustained yield towards the principles of ecosystem-based management (Gauthier et al. 2009; Government of Québec 2010). One key principle of ecosystem-based forest management is to limit the rate of anthropogenic disturbances to conform to the historical ranges of natural variabion in ecosystem properties (Cyr *et al.* 2009), such as species composition and age-class structure. In addition to these new guidelines, permanent and temporary forest blocks (hereafter named protection blocks) have been set aside from logging to improve the conservation of boreal caribou habitat within its actual range (Courtois *et al.* 2004; Équipe de rétablissement du caribou forestier du Québec 2008). Logging activities are therefore permitted in the forest matrix that is located outside protection blocks but their rate, intensity, and spatial distribution are to be informed by historical patterns of natural disturbance regimes (e.g., fire and insect outbreaks). With this management strategy, it is assumed that the substitution of natural for anthropogenic disturbances of the same intensity and rate will maintain species diversity, together with the main ecological functions of ecosystems (Hunter 1993). This assumes that logged and burnt areas are effectively equivalent. Our results show that they are not. Boreal caribou avoided logging areas twice as strongly as burnt areas, even after accounting for many other sources of variation. It follows that logging, at least as it is practised to date, is not equivalent to fire

in terms of its effect on boreal caribou. A possible explanation for the uneven effect of logging and burnt areas on boreal caribou could originate from an increase of road densities that is associated with forest operations, which in turn increases predation risk because roads facilitate the displacement and search efficiency of predators (Houle *et al.* 2010; DeCesare 2012). Thus, substituting burnt areas with equivalent logging areas outside of protection blocks according to current ecosystem-based management guidelines is not likely to maintain the historical suitability of landscapes for boreal caribou. More importantly, wildfires are just as likely to occur within protection blocks as outside them, stressing the need for managing the forest matrix as a whole, including those forest areas that are not targeted for conservation, rather than focusing solely on isolated protection blocks. This study could not address how changes in landscape suitability will affect caribou population dynamics. However, a lower probability of occurrence often translates into decreases in population density (Oliver *et al.* 2012), with evidence showing that logging, more than fire, negatively affects recruitment rate, a key demographic parameter of population rate-of-growth in caribou (Environment Canada 2008, section 6.5). Ecosystem-based management of coniferous boreal forest, therefore, should account for the uneven effect of logging activities compared to that of burnt areas on wildlife species. This point is particularly sensitive given that the co-occurrence and cumulative effects of both disturbance types are expected to persist in the future, despite the delineation of protected areas, since fire control strategies are not one-hundred percent efficient, especially in the far north. Further efforts are urgently needed to characterise the sensitivity of key species to various types of disturbances. Only then will a clearer picture help managers to develop efficient ecosystem-based management guidelines for the boreal forest that properly match conservation planning efforts for boreal caribou.

The strong residual spatial pattern found in the best model reveals some phenomenon or process that we did not include in our models. There is a growing recognition amongst ecologists that the presence of residual spatial autocorrelation is not simply a statistical nuisance (e.g., increasing type-I error). Rather, it may also be an ecological opportunity (McIntire & Fajardo 2009), as it points to an important ecological process(es) that is (are) misspecified or lacking in the given hypothesis or model. While the accounting for spatial

autocorrelation improved the validity of parameter inferences, it should be noted that our results are derived from observational data and, thus, are conditional to the alternative hypotheses that we tested. We argue that identifying patterns of spatial autocorrelation and uncovering their underlying causes are two important steps in understanding which unknown ecological driver(s) structures the spatial distribution of living organisms. The use of an *a posteriori* approach, where spatial dependency is modelled directly from the data, allows the structure of spatial autocorrelation patterns to be explored and provides strong direction for further hypotheses about the underlying causes of species distributions. The distribution of spatial random effects for boreal caribou distinguishes a zone of high connectivity with a high potential conservation value along 70° of longitude. Causes of this pattern are unknown, but our study allowed us to discount habitat variables and climate normals as possible drivers, since these covariates were already included in our model. We propose two hypotheses to explain this spatial pattern: behaviour-driven and history-driven hypotheses. The behaviour-driven hypothesis considers that the actual latent pattern reflects the meta-population structure of the different boreal caribou herds in the region and may depict zones of intensive exchanges amongst populations. The history-driven hypothesis postulates that historical factors associated with range fidelity have shaped the spatial distribution of boreal caribou populations over time and that the actual latent spatial pattern is a relic of this evolution. These two hypotheses could be separated based on their expected spatial patterns, according to the approach advocated by McIntire & Fajardo (2009). Our study provides a starting point, but further studies will be needed to validate or refute these hypotheses.

Acknowledgements

References

Ashton KG, Tracy MC, Queiroz AD (2000) Is Bergmann's Rule valid for mammals? American Naturalist 156: 390-415.

Balshi MS, McGuire AD, Duffy P, Flannigan M, Walsh J, et al. (2009) Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. Global Change Biology 15: 578-600.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, et al. (2011) Has the Earth's sixth mass extinction already arrived? Nature 471: 51-57.

Bastille-Rousseau G, Dussault C, Couturier S, Fortin D, St-Laurent M-H, Drapeau P, Dussault C, Brodeur V (2012). Sélection d'habitat du caribou forestier en forêt boréale québécoise, Québec, ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, Direction générale de l'expertise sur la faune et ses habitats, 66 p.

Bergeron Y, Gauthier S, Flannigan M, Kafka V (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Québec. Ecology 85: 1916-1932.

Bouchard M, Pothier D, Gauthier S (2008) Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Canadian Journal of Forest Research 38: 1621-1633.

Boulet M, Couturier S, Côté SD, Otto RD, Bernatchez L (2007) Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. Molecular Ecology 16: 4223-4240.

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 (COSEWIC), Ottawa, ON.

Courbin N, Fortin D, Dussault C, Courtois R (2009) Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. Landscape Ecology 24: 1375-1388.

Courtois R, Gingras A, Dussault C, Breton L, Ouellet J-P (2003) An aerial survey technique for the forest-dwelling ecotype of woodland caribou, *Rangifer tarandus caribou*. Canadian Field-Naturalist 117: 546-554.

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Courtois R, Ouellet J-P, Dussault C, Gingras A (2004) Forest management guidelines for forest-dwelling caribou in Québec. Forestry Chronicle 80: 598-607.

Courtois R, Gingras A, Fortin D, Sebbane A, Rochette B, et al. (2008) Demographic and behavioural response of woodland caribou to forest harvesting. Canadian Journal of Forest Research 38: 2837-2849.

Couturier S, Otto RD, Côté SD, Luther G, Mahoney SP (2010) Body size variations in caribou ecotypes and relationships with demography. Journal of Wildlife Management 74: 395-404.

Cyr D, Gauthier S, Bergeron Y, Carcaillet C (2009) Forest management is driving the eastern North American boreal forest outside its natural range of variability. Frontiers in Ecology and the Environment 7: 519-524.

DeCesare N J (2012) Separating spatial search and efficiency rates as components of predation risk. Proceedings of the Royal Society B: Biological Sciences 279: 4626-4633.

Dussault C, Pinard V, Ouellet J-P, Courtois C, Fortin D (2012) Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? Proceedings of the Royal Society B: Biological Sciences 279: 4481-4488.

Dyer SJ, O'Neill JP, Wasel SM, Boutin S (2001) Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65: 531-542.

Environment Canada (2008) Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Environment Canada, Ottawa, ON.

Environment Canada (2011) National Climate Data and Information Archive. http://climate.weatheroffice.gc.ca/

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 + 138pp.

Équipe de rétablissement du caribou forestier du Québec (2008) Plan de rétablissement du caribou forestier (*Rangifer tarandus*) au Québec – 2005-2012. Ministère des Ressources naturelles et de la Faune, Faune Québec, Direction de l'expertise sur la faune et des habitats, Canada. [In French.]

Faille G, Dussault C, Ouellet J-P, Fortin D, Courtois R, St-Laurent M-H, Dussault C (2010) Range fidelity: The missing link between caribou decline and habitat alteration? Biological Conservation 143: 2840-2850.

Festa-Bianchet M, Ray JC, Boutin S, Côté SD, Gunn A (2011) Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Canadian Journal of Zoology 89: 419-434.

Fortin D, Courtois R, Etcheverry P, Dussault C, Gingras A (2008) Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. Journal of Applied Ecology 45: 1392-1400.

Fortin D, Buono P-L, Fortin A, Courbin N, Gingras CT, Moorcroft PR, Courtois R, Dussault C (2013) Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. American Naturalist 181: 827-836.

Fortin M-J, Dale MRT (2005) Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, UK.

Gauthier S, Vaillancourt M-A, Leduc A, De Grandpré L, Kneeshaw D, et al. (2009) Ecosystem management in the boreal forest. Presses de l'Université du Québec, Québec, QC, Canada.

Government of Québec (2010) Loi sur l'aménagement durable du territoire forestier. Éditeur officiel du Québec. Gouvernement du Québec.

Herfindal I, Solberg E, Sæther B-E, Høgda K, Andersen R (2006) Environmental phenology and geographical gradients in moose body mass. Oecologia 150: 213-224.

Houle M, Fortin D, Dussault C, Courtois R, Ouellet JP (2010) Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. Landscape ecology 25: 419-433.

Hunter Jr ML (1993) Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65: 115-120.

Intergovernmental Panel on Climate Change - IPCC (2007) Climate Change 2007: Synthesis Report. Core Writing Team, R. K. Pachauri, and A. Reisinger, Eds., IPCC, 104 pp.

Levin SA (1992) The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology 73: 1943-1967.

MacArthur RH (1972) Geographical Ecology. Harper & Row. New York, New York, USA.

McIntire EJB, Fajardo A (2009) Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90: 46-56.

McKenney DW, Pedlar JH, Papadopol P, Hutchinson MF (2006) The development of 1901–2000 historical monthly climate models for Canada and the United States. Agricultural and Forest Meteorology 138: 69-81.

Ministère des ressources naturelles et de la Faune du Québec (2003) Normes de cartographie écoforestière du troisième inventaire écoforestier. Forêt Québec. Direction des inventaires forestiers. ISBN 2-551-xxxxx-x. 109 p. [in French]

Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136: 1-13.

Oliver TH, Hill JK, Thomas CD, Brereton T, Roy DB (2009) Changes in habitat specificity of species at their climatic range boundaries. Ecology Letters 12: 1091–1102.

Oliver TH, Gillings S, Girardello M, Rapacciuolo G, Brereton TM, et al. (2012) Population density but not stability can be predicted from species distribution models. Journal of Applied Ecology 49: 581-590.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, et al. (2010) Scenarios for global biodiversity in the 21st century. Science 330: 1496-1501.

Post E (2005) Large-scale spatial gradients in herbivore population dynamics. Ecology 86: 2320-2328.

R Development Core Team (2011) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466–478.

Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 71: 319-392.

Schaefer JA, Pruitt WO (1991) Fire and woodland caribou in southeastern Manitoba. Wildlife Monographs 116: 1–39.

Schaefer JA (2003) Long-term range recession and the persistence of caribou in the taiga. Conservation Biology 17: 1435-1439.

Sharma S, Couturier S, Côté, SD (2009) Impacts of climate change on the seasonal distribution of migratory caribou. Global Change Biology 15: 2549-2562.

Thomas DC, Edmonds EJ, Brown WK (2011) The diet of woodland caribou populations in west-central Alberta. Rangifer 16: 337-342.

Thuiller W, Araújo MB, Lavorel S (2004) Do we need land-cover data to model species distributions in Europe? Journal of Biogeography 31: 353-361.

Thuiller W (2007) Biodiversity: Climate change and the ecologist. Nature 448: 550-552.

Vors LS, Schaefer JA, Pond BA, Rodgers AR, Patterson BR (2007) Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. Journal of Wildlife Management 71: 1249-1256.

Vors LS, Boyce MS (2009) Global declines of caribou and reindeer. Global Change Biology 15: 2626-2633.

Wasser SK, Keim JL, Taper ML, Lele SR (2011) The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. Frontiers in Ecology and the Environment 9: 546-551.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer Science, New York, USA.

Appendices

Appendix 2.1: Classification of variables based on forest inventory mapsheets

Appendix 2.2: Loadings from Principal Component analysis.

Appendix 2.3: Additional information on statistical models.

Appendix 2.4: Model selection and spatial autocorrelation.

Appendix 2.5: Inference and residual spatial autocorrelation.

Appendix 2.1. Classification of variables based on information provided by forest inventory mapsheets

Variable	Main codes used in forest inventory mapsheets
Water bodies	ter_co = 'EAU' OR ter_co = 'INO'
Wetlands	ter_co = 'DH'
Lichen heaths	ter_co = 'DS' AND psc_co = 'C'
Lichen woodland	ter_co NOT IN('DS') AND (psc_co = 'C' OR tec_co_tec IN('RE11', 'RE12', 'RE13', 'RE14', 'RE15', 'RE16'))
Burnt areas	((cha_co > 4) OR (cha_co IS NULL)) AND per_co_ori = 'BR'
Logging areas	((cha_co > 4) OR (cha_co IS NULL)) AND per_co_ori IN('CBA','CBT','CEF','CPE','CPH','CPR','CPT','CRB','CRR','CRS', 'CT','DT','ENM','ENS','ETR','FR','P','PLN','PLR','PRR','RIA','RPS')
Deciduous stands	ges_co IN('ALM','BB1E','BB1PG','BB1R','BB1S','BBBBE','BBBBPG','BBBBR','BBBBS','BBE','BBEPL','BBEPN','BBPB','BBPEE','BBPEPG','BBPER','BBPES','BBPG','BBR','BBS','BJR','BJ+R','BJBJRX','BJBJSB','BJBPRX','BJBPSB','BJPESB','BPBJSB','BPBPEN','BPBPEP','BPBPPG','BPBPRX','BPBPSB','BPEOSB','BPPEEN','BPPEEP','BPPEPG','BPPERX','BPPESB','EOBPEN','EOBPSB','EOPESB','EOR','ERBPSB','EREOSB','ERR','FEPH','FEPL','FEPN','FHFIRX','FHPESB','FHR','FIBBE','FIBBPG','FIBBR','FIBBS','FIBPEN','FIBPRX','FIBPSB','FIE','FIEPL','FIEPN','FIEPO','FIPEE','FIPEEN','FIPEPG','FIPER','FIPERX','FIPES','FIPESB','FIPG','FIPIG','FIR','FIRES','FIS','FMEL','FNC','FPIG','FTR','FXEB','FXEN','FXEPL','FXEPN','FXEPO','FXEV','FXFXRX','FXPG','FXPIG','FXRX','MF','PE1E','PE1R','PE1S','PEBBE','PEBBPG','PEBBR','PEBBS','PEBPEN','PEBPEP','PEBPPG','PEBPRX','PEBPSB','PEE','PEEOSB','PEEPN','PEPB','PEPEE','PEPEEN','PEPEEP','PEPEPB','PEPEPG','PEPEPR','PEPER','PEPERX','PEPES','PEPESB','PEPG','PEPIG','PER','PERES','PES','PTBPRX')
Mixed deciduous stands	ges_co IN('ALM','BB1E','BB1PG','BB1R','BB1S','BBBBE','BBBBPG','BBBBR','BBBBS','BBE','BBEPL','BBEPN','BBPB','BBPEE','BBPEPG','BBPER','BBPES','BBPG','BBR','BBS','BJR','BJ+R','BJBJRX','BJBJSB','BJBPRX','BJBPSB','BJPESB','BPBJSB','BPBPEN','BPBPEP','BPBPPG','BPBPRX','BPBPSB','BPEOSB','BPPEEN','BPPEEP','BPPEPG','BPPERX','BPPESB','EOBPEN','EOBPSB','EOPESB','EOR','ERBPSB','EREOSB','ERR','FEPH','FEPL','FEPN','FHFIRX','FHPESB','FHR','FIBBE','FIBBPG','FIBBR','FIBBS','FIBPEN','FIBPRX','FIBPSB','FIE','FIEPL','FIEPN','FIEPO','FIPEE','FIPEEN','FIPEPG','FIPER','FIPERX','FIPES','FIPESB','FIPG','FIPIG','FIR','FIRES','FIS','FMEL','FNC','FPIG','FTR','FXEB','FXEN','FXEPL','FXEPN','FXEPO','FXEV','FXFXRX','FXPG','FXPIG','FXRX','MF','PE1E','PE1R','PE1S','PEBBE','PEBBPG','PEBBR','PEBBS','PEBPEN','PEBPEP','PEBPPG','PEBPRX','PEBPSB','PEE','PEEOS

	B','PEEPN','PEPB','PEPEE','PEPEEN','PEPEEP','PEPEPB','PEPEPG','PEPEPR','PEPER','PEPERX','PEPES','PEPESB','PEPG','PEPIG','PER','PERES','PES','PTBPRX')
Mixed coniferous stands	ges_co IN('EBB','EBFX','EBFZ','EFI','ENENBJ','ENENBP','ENENFI','ENENFX','ENENPE','ENFX','ENFZ','ENPBBP','ENPGBP','ENPGPE','ENSBBP','ENSBEO','ENSBFX','ENSBPE','EPE','EPEP','EPEPBP','EPEPFI','EPEPPE','EPHF','EPLF','EPLFI','EPLFX','EPNF','EPNFI','EPNFX','EPOBP','EPOFX','EPSBBP','EVFX','EVFZ','MELF','MR','MX','PBBB','PBFI','PGBB','PGENBP','PGENPE','PGFI','PGFX','PGFZ','PGPE','PGPGBP','PGPGPE','PIGBB','PIGF','PIGFI','PIGFX','PIGPE','RBB','RBJ','RBJ+','REO','RESFI','RFH','RFI','RFT','RPE','RX','RXFX','RXRX','RXRXBP','RXRXFI','RXRXFX','RXSBBP','SBB','SBENBJ','SBENBP','SBENEO','SBENFH','SBENFI','SBENPE','SBPBBP','SBSBBJ','SBSBBP','SBSBEO','SBSBFI','SBSBFX','SBSBPE','SFI','SPE)
Jack Pine	ges_co IN('PB','PBPB','PBPG','PBSB','PG','PGPB','PGPG','PGS','PIB','PIG','PIGPIR','PIGR','PIR','PIRR','PIS','RPG','RPIG','RXPB','RXPG')
Black spruce	ges_co IN('EC','EE','EEC','EEPN','EG','EME','EN','ENEN','ENML','EPN','EPNEPL','EPNR','EU','EV','ME','MEL','MEME','MLEN','RC','RE','REPL','REPN','RES','RME','RXEN')
Black spruce - Jack Pine	ges_co IN('PGE','PBE','PBEN','EPG','PGEN','PGME','PIGE','PIGEPL','PIGEPN','ENPB','ENPG','EPHPIG','EPLPIG','ENPB','EPNPG','EPNPIG','EPNPIR','MEPG')
Black spruce – Balsam fir	ges_co IN('EPNS','EPNSAB','EPSB','ES','ESAB','ENSB','ENTO','TOEN','SABE','SABEPN','SBEN','SBEP','SE','SEPN','SME','CE','CME','MES)
Balsam fir	ges_co IN('CS','EB','EBPG','EBRX','EBSB','EPB','EPH','EPL','EPLEPN','EPLR','EPO','RG','RS','RXEB','RXSB','RXTO','SB','SBPB','SBSB','SBSE','SC','SPB','SPG','SS','SSAB','TOSB','TOTO')

Note 1: To limit the number of different stand types in the statistical analyses, we have grouped all stands (forested polygons) into eight main stand groups (see variables in the table above). Numerous species combination codes (ges_co) were found in only a few stands (polygons) and their combined area was negligeable at the scale of this study. Therefore, these rare stands were merged with one of the eight stand variables that exhibited the highest similarity in terms of ecological characteristics.

Note 2: The full SQL request for the classification of variables accounted for :
1) the time lag between the inventory year of each caribou block and the date at which forest data were updated.
2) stand heigth
3) the year of disturbance

Note 3: For description of all codes, refer to *Ministère des ressources naturelles et de la Faune du Québec (2003) Normes de cartographie écoforestière du troisième inventaire écoforestier. Forêt Québec. Direction des inventaires forestiers. ISBN 2-551-xxxxx-x. 109 p. [in French]*

Appendix 2.2. Loadings from Principal Component analysis

Table S1. Loadings of explanatory variables related to conifer stands on the first two dimensions of a Principal Component analysis across the study area in Québec, Canada.

	PCA1	PCA2
black spruce - jack pine	-0.15	-0.01
black spruce	0.07	**-0.99**
black spruce - balsam fir	**0.98**	0.06
balsam fir	0.09	0.07
jack pine	-0.04	0.01
mixed coniferous	-0.02	0.04
Eigenvalues	15.56	14.85
Percentage variance	46.93	42.74
Cumulative percentage variance	46.93	89.67

Appendix 2.3. Additional information on statistical models

Although we used the same data as Fortin *et al.* (2008) to document the presence of boreal caribou tracks, our modelling approach and covariates differed markedly from theirs (e.g., their model did not include any climate variables). The use of regular lattice-based models, together with up-to-date forest inventory data, allowed us to obtain new inferences on climate, vegetation attributes, and disturbances. In addition, we used different statistical models with (i) a random intercept model to account for the spatio-temporal structure of inventory aerial blocks imposed by our design and (ii) a spatial random effect, instead of an autocovariate term in a fixed effect autologistic model, to account for spatial autocorrelation. Given the differences in approach between Fortin *et al.* (2008) and the present study, differences in the results are expected. To ensure, however, that the presence of geographical gradients in the selection of certain habitat classes was present in our data and not simply the result of a statistical artefact, we compared a model with only linear effects of covariates on a logit scale (model 3; Table 2.3) with a model with the same covariates but containing interaction terms between covariates and latitude/longitude (model 6; Table 2.3). Interaction terms were selected using a screening process where only significant interaction terms (e.g., credible intervals of parameters not overlapping zero) between covariates and latitude/longitude (in UTM coordinates) were retained using a backwards, stepwise procedure.

References:

Fortin D, Courtois R, Etcheverry P, Dussault C, Gingras A (2008) Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. *Journal of Applied Ecology*, **45**, 1392-1400.

Appendix 2.4. Model selection and spatial autocorrelation

Model comparisons and inference can be invalidated by the presence of spatial autocorrelation in model residuals. Bayesian analyses offer a flexible framework for fitting hierarchical spatial models, e.g., spatial GLMM (generalised linear mixed-models), especially since fast and accurate Bayesian approximations are now freely available (Rue *et al.* 2009) and greatly reduce computational demands. Deviance Information Criterion (DIC) is commonly used to compare the fit of alternative Bayesian models under the parsimony principle (Spiegelhalter *et al.* 2002), but theoretical foundations of DIC-comparisons have little support for this class of models (Plummer 2008) and can even lead to poor conclusions when the goal is to compare the importance of different environmental covariates among models. We thus constrained our model selection procedure to non-spatial GLMMs, as described in Equation 1. We verified if spatial autocorrelation had an impact on the model selection procedure. To do so, we randomly selected 20% of cells in the original data set using a stratified sampling scheme with survey blocks as strata. The mean Euclidean distance between sampled cells and their four sampled nearest-neighbours increased from 10 km in the whole data set to ~21 km in data subsets. This intensity of subsampling is expected to remove or reduce spatial auto-correlation in the original data set. We repeated this operation to produce 1000 independent subsamples and then fitted each candidate model to each data subset and calculated the frequencies of the best-ranked models over the 1000 trials. Finally, we compared the frequencies of the best-ranked models over the 1000 trials with the rank of candidate models obtained with 100% of the data. Difference in the model ranking between these two methods would indicate that spatial autocorrelation impacts the model selection procedure with 100% of the data. The graph below (Figure S3) shows that the rank order of selection frequencies as top models among the 1000 subsamples match almost perfectly the same as the ordering of model DIC in Table 2.2. We conclude that spatial autocorrelation only had a negligible effect on the result of the model selection procedure.

Figure S3. Bar plot showing the frequency of top-ranked models selected over the 1000 random subsamples (20% of the data each). Red number at the top of each bar represents the rank order of the best model with 100% of the data (see Table 2.3).
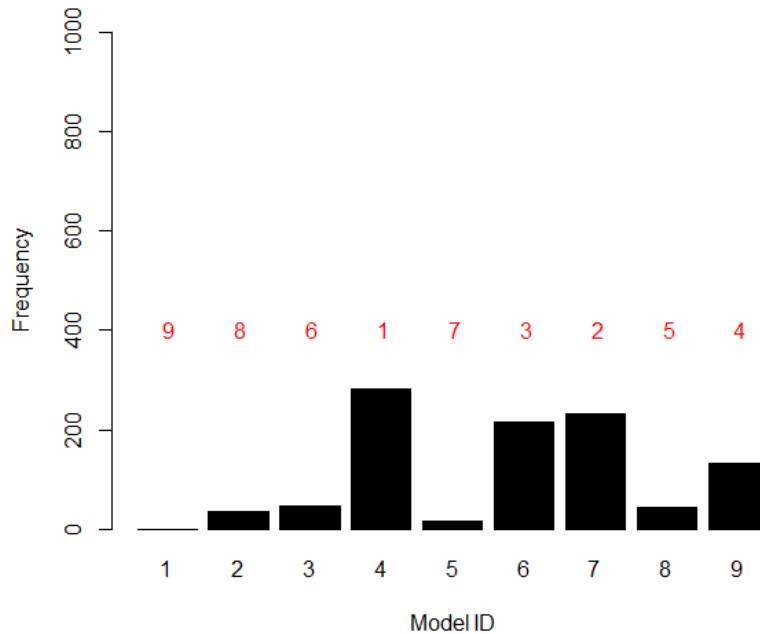
References

Plummer M (2008) Penalized loss functions for Bayesian model comparison. *Biostatistics*, **9**, 523-539.

Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **71**, 319-392.

Spiegelhalter DJ, Best N, Carlin B, van der Linde A (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **64**, 583-640.

Appendix 2.5. Inference and residual spatial autocorrelation

In addition to model selection and hypothesis tests, we were also interested in making inference on parameters. For inference, we used the complete data set, together with the simplest and top-ranked model that had been selected in the previous step (see model 4 in Table 2.2). To avoid type-I error caused by residual spatial autocorrelation, we modelled spatial autocorrelation among cells using a Markov representation on a regular grid of a continuous Gaussian field with a Matérn covariance function such as:

$$Corr(d) \propto (\kappa d)^{\nu} \, K_{\nu}(\kappa d)$$

Where d is the Euclidean distance, $K_{\nu}()$ is the Bessel function of order ν. The range is defined to be $\sqrt{8}/\kappa$ and it is the distance at which two cells are practically uncorrelated. This Matérn function is defined by two hyperparameters: the range (r) and the precision (τ). The range defines the distance at which two cells become uncorrelated, while the precision defines the degree of smoothness of the spatial random effect. Based on the variogram of the residuals of the non-spatial GLMM, we fixed the range to be nine times the distance between two neighbouring cells. The Matérn covariance function implies a dense covariance matrix that greatly increases computational demands and processing time (Minasny & McBratney 2005). The INLA software uses a Markov representation of the Matérn field which was introduced by Lindgren *et al.* (2011). The Markov representation offers several computational advantages and greatly reduces the running time to fit such model (see Lindgren *et al.* 2011). Based on sensitivity analyses (Figure S4), we assigned the precision a Gamma(shape = 29, scale = 0.001) to avoid overfitting (Beguin *et al.* 2012). A sum-to-zero constraint was applied to the estimation of the spatial random effect to ensure parameter identifiability.

Figure S4. Sensitivity analyses regarding the effect of various shape parameters on coefficients of regression (median ± 95% credible interval). Increasing the value of the shape parameter leads to decreasing smoothness of the spatial random effect. When the shape parameter > 29.56, spatial models (white dots) become equivalent to non-spatial models (black dots). Note that the scale of y-axis differs among plots and that the scale of x-axis is interrupted above 29.
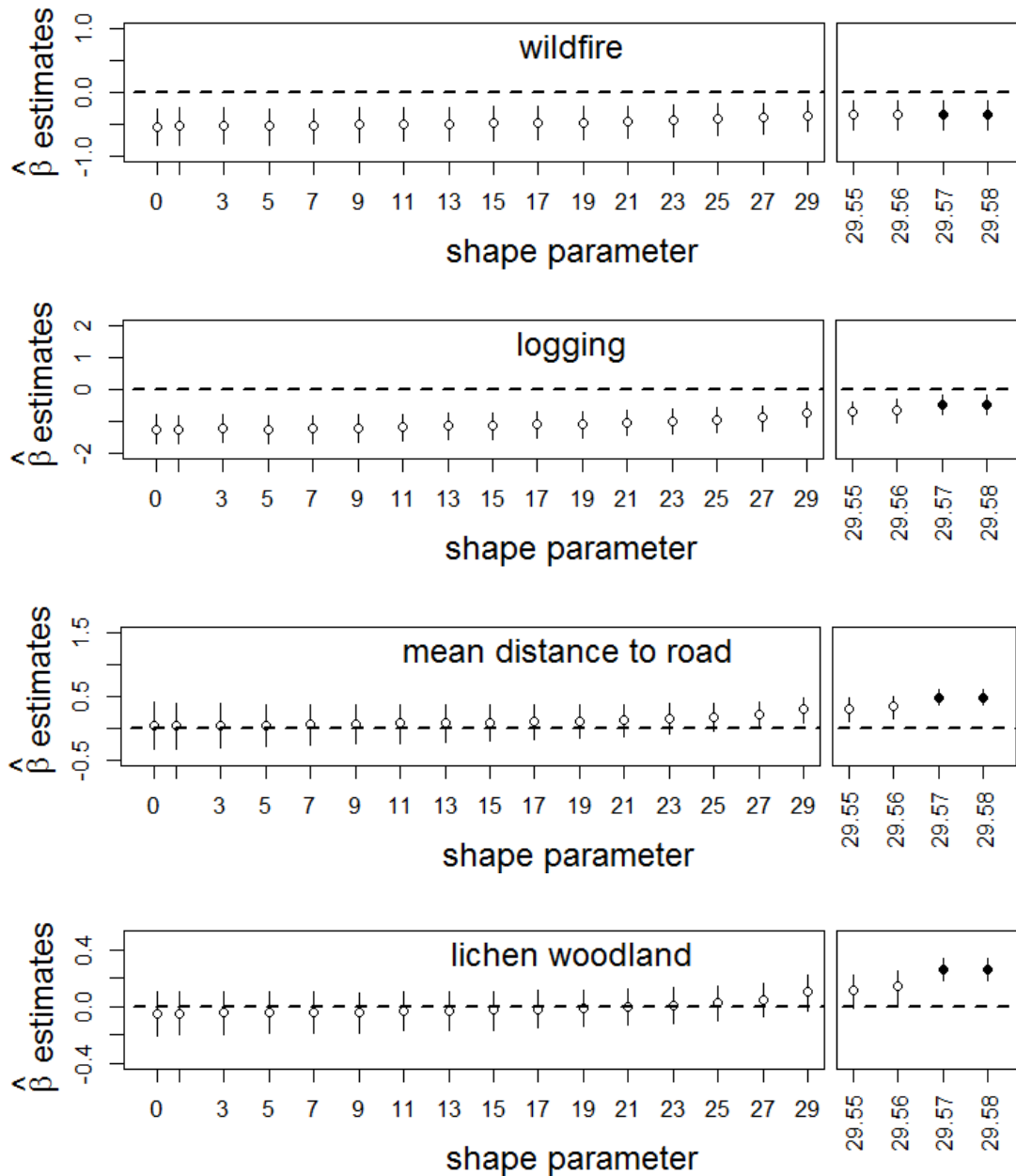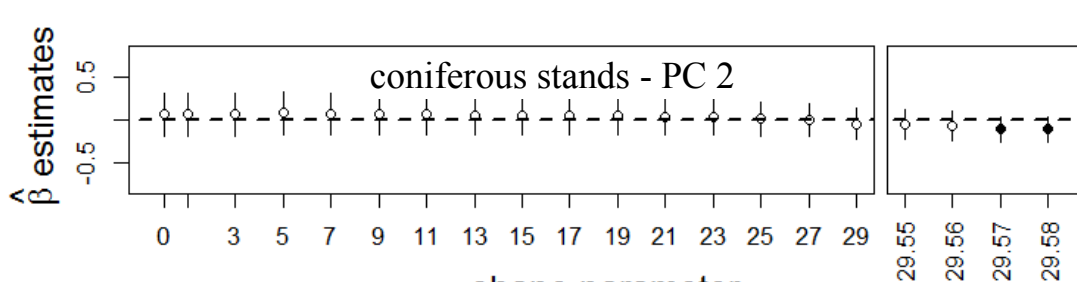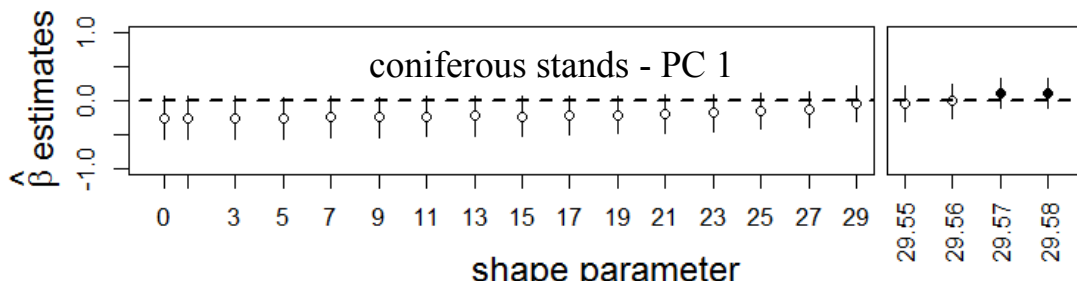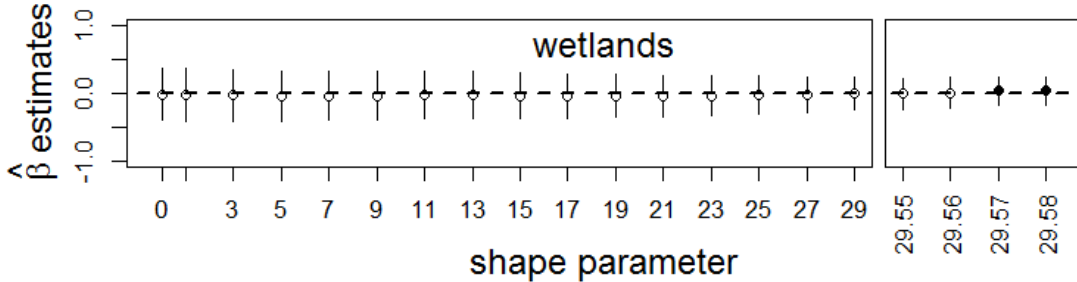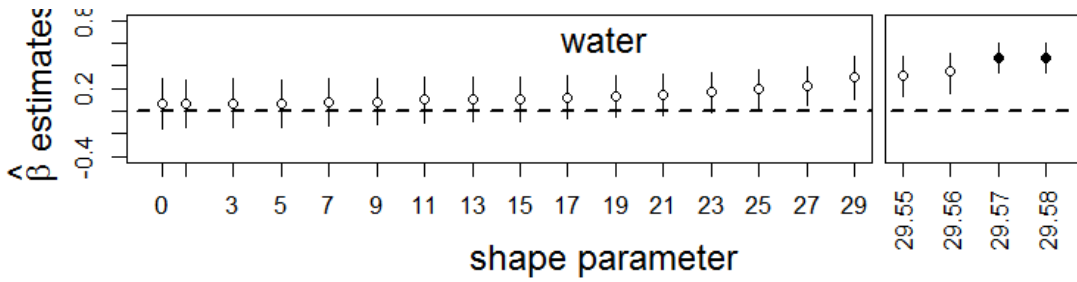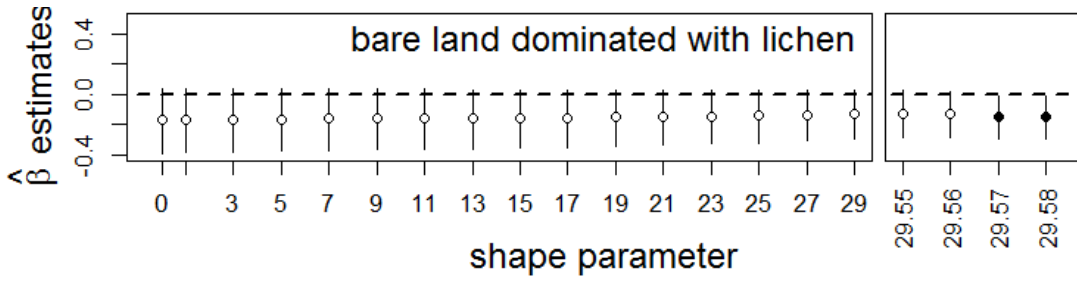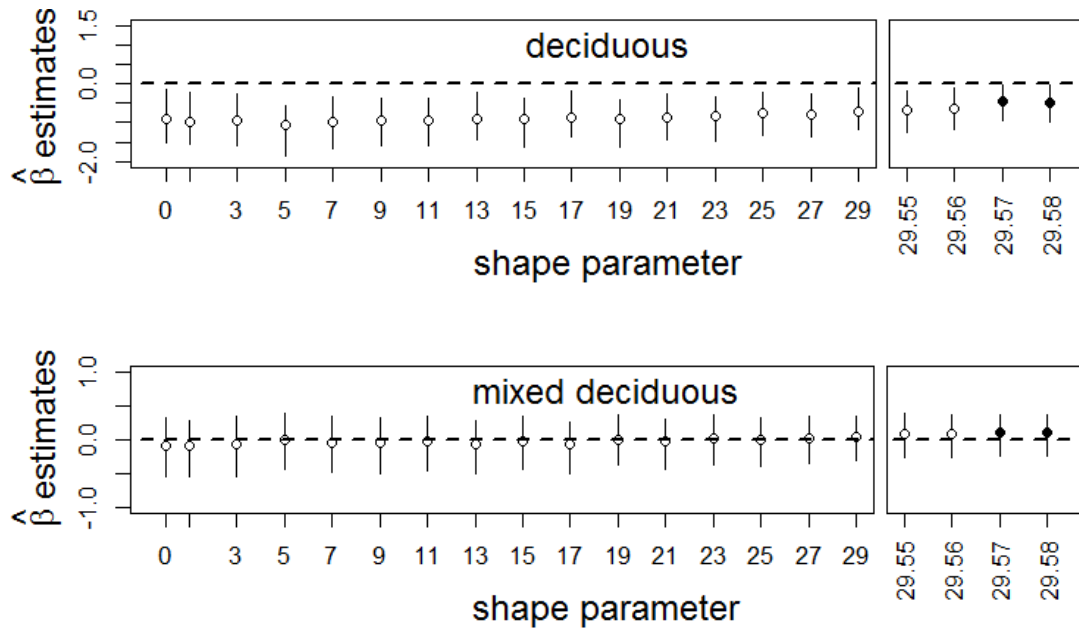
References

Beguin J, Martino S, Rue H, Cumming SG (2012) Hierarchical analysis of spatially autocorrelated ecological data using integrated nested Laplace approximation. *Methods in Ecology and Evolution*, **3**, 921-929.

Lindgren F, Lindstrøm J, Rue H (2011) An explicit link between Gaussian fields and Gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **73**, 423-498.

Minasny B, McBratney AB (2005) The Matérn function as a general model for soil variograms. *Geoderma*, **128**, 192-207.

CHAPITRE 3:

DYNAMICS OF WILDLIFE CONSERVATION - FORESTRY CONFLICTS UNDER FIRE RISK: LESSONS FROM THE THREATENED CARIBOU IN EASTERN CANADA.

JULIEN BEGUIN, ELIOT J.B. MCINTIRE & FRÉDÉRIC RAULIER

Résumé

L'utilisation des réseaux d'aires protégées est la principale approche utilisée en conservation à l'échelle mondiale pour protéger la biodiversité. Toutefois, peu d'information est disponible quant à l'efficacité d'une telle approche dans des écosystèmes dynamiques en termes de conservation et de coût/bénéfices socio-économiques. Dans cette étude, nous avons utilisé le cas du caribou forestier (*Rangifer tarandus caribou*) dans la forêt boréale aménagée de l'est du Canada pour évaluer l'efficacité économique et biologique du réseau actuel d'aires protégées en relation avec l'approvisionnement en matière ligneuse et le risque de feu de forêt. Nous avons mis en œuvre une expérience factorielle à partir d'un modèle de simulation des paysages spatialement explicite pour quantifier les effets des réseaux d'aires protégés, de la foresterie industrielle, des régimes de feu, ainsi que leurs interactions, sur la dynamique de population du caribou forestier et sur les coûts économiques reliés à l'aménagement forestier. Nos résultats ont montré que le feu augmentait les antagonismes entre la conservation du caribou forestier et l'aménagement forestier. Bien qu'une augmentation des aires protégées aidait à réduire les effets négatifs de la récolte forestière sur le caribou forestier, nous avons démontré que les niveaux actuels de récolte en matière ligneuse qui sont planifiés étaient surestimés et ne permettaient ni un approvisionnement durable en matière ligneuse pour l'industrie forestière, ni le maintien à long terme d'une qualité suffisante des paysages pour maintenir le caribou forestier. L'utilisation de coupes de récupération après feu n'a pas pu empêcher des ruptures d'approvisionnement en matière ligneuse. De plus, les coûts associés à ce type de coupe étaient élevés et très variables ce qui limite les bénéfices économiques des coupes de récupération après feu à des régions situées proches des routes et des usines de transformation du bois. En conclusion, nos résultats ont montré que la politique actuelle n'est très probablement pas durable tant pour la conservation du caribou forestier que pour l'approvisionnement en bois pour l'industrie forestière et nous suggérons de tester des politiques alternatives quant à l'organisation des aires de conservation et de la planification de l'aménagement forestier afin d'atteindre un meilleur compromis entre conservation et exploitation forestière.

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Abstract

Protected area networks are the dominant conservation approach used worldwide for protecting biodiversity. Little is known, however, about the efficiency of current protected area networks in dynamic ecosystems in terms of conservation and socio-economic values. In this study, we used a case study with the threatened forest-dwelling caribou (*Rangifer tarandus caribou*), hereafter boreal caribou, in the managed boreal forests of eastern Canada to assess the biological and economic effectiveness of current conservation planning in relation to timber supply for the forest industry and fire risk. We used a spatially explicit landscape simulation model together with a factorial experiment to evaluate the effects of protected area networks, industrial forestry, fire regimes and their interactions on the population dynamics of boreal caribou and the economic costs related to forest management. Our results showed that fire increased conflicts between achieving current levels of timber harvest and habitat conservation of boreal caribou in the eastern boreal forest of Canada. Although increasing conservation areas helped reducing the negative impacts of timber harvest on boreal caribou, we demonstrated that current planned harvest levels were overestimated and could neither provide a sustainable timber supply for the forest industry, nor ensure long term landscape suitability for boreal caribou persistence. Salvage logging could not prevent the occurrence of critical periods with shirtfalls in the level of realized harvest volume. Furthermore, costs associated with salvage logging were also high and exhibited considerable variation which limits any economic benefits of salvage logging to areas located close to existing roads and mills. Overall, our results indicated that the current policy is unlikely to be sustainable for either boreal caribou conservation or timber supply and we suggested testing possible alternatives in the organization of conservation and forest management planning to achieve better trade-offs between conservation and timber harvesting.

Introduction

Protected area networks are the dominant conservation approach used worldwide for protecting biodiversity (Millennium Ecosystem Assessment 2005). Conservation planning in managed forests, however, represents many challenges worldwide when species to be protected use mature forest stands targeted by the forest industry for timber supply. On one hand, prohibition of timber harvest within protected areas may carry high economic opportunity costs (i.e. the loss of potential economic gain from forest industry when protection is chosen), and on the other hand, the absence of restriction in timber harvest may result in habitat and species losses. Spotted owl (*Strix occidentalis*) management in western US is a flagship case study illustrating the challenge to reconcile conservation and management of old-growth forests (Gutiérrez 2008). Similar challenges arose in many places around the world such as the conservation of specialized woodpeckers in hemiboreal forests of Europe (Roberge *et al.* 2008), the conservation of Giant Panda (*Ailuropoda melanoleuca*) in interior forests of the Republic of China (Bearer *et al.* 2008) or the conservation of the endangered boreal woodland caribou (*Rangifer tarandus caribou*) in boreal forest of Canada (Schneider *et al.* 2010), to name a few.

Optimization techniques are often used to allocate efficiently conservation resources and to delimit optimal protected area networks given a set of constraints (e.g. budget and opportunity costs) (Wilson *et al.* 2006). Using optimization, Schneider *et al.* (2012) identified that sixty percent of the current boreal woodland caribou range in Alberta could be protected while maintaining access to over 98% of the value of natural resources. But, forestry was not the main commercial activity in their study and they did not explicitly include the fire regime, making unclear whether or not fire influenced the spatial distribution of opportunity costs over time. Hauer *et al.* (2010) also used optimization and accounted for the fire regime in their trade-off analyses between forestry and conservation objectives but they did not investigate the effect of different protected area networks on conservation and economic indicators. Conservation planning is inherently a spatial process occurring in dynamic environments and protected area networks can yield contrasted costs and benefits at different spatial and temporal scales (Naidoo *et al.* 2006). Tittler *et al.* (2012) found that concentrating anthropogenic disturbance through zoning and using

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intensive forest management on a small part of the landscape may counterbalance the negative effects for the industry of increasing protected areas at larger scale. However, we ignore in most cases the biological and economic effectiveness of current conservation planning in relation to industrial forestry and fire risk. In ecosystems shaped by fire, the benefits of protected areas may be transitory and last for a limited, often unpredictable, period of time. Thus, quantifying the efficiency of current protected area networks in dynamic ecosystems in terms of conservation and socio-economic values at various spatiotemporal scales is a critical step for informing sound conservation policies. Furthermore, a transparent multi-scale assessment of conservation and economic values also has the potential to lower human-wildlife conflicts in current conservation practices by filling an important gap between ecology and economy (Redpath *et al.* 2012).

Boreal forests are dynamic ecosystems where large natural disturbances play an important role in landscape dynamic (Bergeron *et al.* 2004) and may impose important constraints on both conservation and forest management. From a management point of view, fires often cause timber losses for the industry in the short and medium terms. Paradoxically, fires also make large amount of timber volume readily available for a very short time via salvage logging. Costs and benefits of this type of logging, however, greatly depend on the spatial characteristics of landscape elements such as the development of road network and protected areas. For instance, the spatial configuration of protected areas may alter the spreading of the road network and induce additional timber transportation costs. From a conservation point of view, fires may occur inside protected areas, which decrease their benefits. This is exacerbated by the fact that the amount of logging area usually is additive with the amount of area burned (Bergeron *et al.* 2006), increasing the amount of total disturbance at the landscape level. This can have strong negative effects on vital rates of endangered species that depend on intact forest, such as boreal caribou (Courtois *et al.* 2007; Sorensen *et al.* 2010; Environment Canada 2012).

In this study, we used the threatened forest-dwelling caribou or boreal woodland caribou (hereafter "boreal caribou") in the managed boreal forests of eastern Canada as a case study to assess the biological and economic effectiveness of current conservation planning in

relation to timber supply and fire risk. More precisely, our main study objective was to understand how the effects of protected area networks, industrial forestry, fire regimes and their interactions shape the population dynamics of boreal caribou and the economic costs related to forest management. We distinguished two types of conservation area in the study region: traditional permanent protected areas such as defined by IUCN and caribou specific protection blocks. The former are created by the province of Quebec as part of a general strategy to protect natural areas and the latter are designed to specifically address the needs of boreal caribou (Courtois *et al.* 2004). We first assessed how increasing the amount of conservation areas affected planned timber harvest levels in three different forest management units of $>10^4$ km^2 each and what were the consequences in terms of transportation-related costs. This allowed us to quantify the economic consequences for the forest industry of such policy and to test the hypothesis that spatial arrangement of conservation areas over the landscapes increased transportation costs at large spatial scale for the forest industry. Second, we assessed the separate and joint impacts of fire, logging and road network on the annual population growth rate of boreal caribou under various levels of protection. This allowed us to quantify the ecological consequences of timber harvest and wildfires on boreal caribou demography under various conservation schemes. Experimental manipulation of these processes at a large spatial scale is impossible in practice, so we controlled the amount and distribution of protected areas, logging, fire, and roads using a spatially explicit landscape simulation model in which each of these processes were interrelated. We designed a 3x3 factorial experiment where three different conservation scenarios interacted with three different forest management scenarios to cover a wide range of combinations among these processes. Based on the results of economic and ecological indicators of each scenario combination, we discuss the efficiency of current conservation planning for boreal caribou in managed boreal forests.

Methods

Study area

The study region (38844 km^2) is located in the coniferous boreal forest of eastern Canada (Fig. 3.1), within the south-eastern range of forest-dwelling caribou in the Province of Québec. The study area is part of the Côte-Nord, an administrative region located in the eastern part of the province.
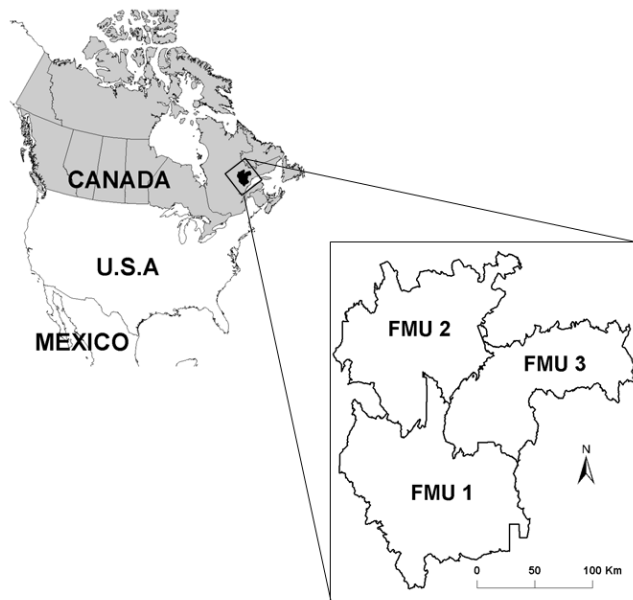
Figure 3.1. Location of the study area and the three forest management units (FMUs) used in our simulation model (see Table 3.1 for further descriptions).

Soil and climate conditions are described in detail in Bouchard *et al.* (2008a). Forested areas represent 76% of the study region (Table 3.1) and are dominated by coniferous stands in which black spruce (*Picea mariana* (Miller) BSP) and balsam fir (*Abies balsamea* (L.) Miller) are the most frequently encountered tree species (Table 3.1), followed by Jack pine (*Pinus banksiana* Lambert) (Table 3.1).

Table 3.1. Initial characteristics of landscapes and land allocation for the three forest management units in this study.

Class	Variables	FMU 1 (09351)		FMU 2 (09352)		FMU 3 (09452)		Total	
		(km^2)	(%)	(km^2)	(%)	(km^2)	(%)	(km^2)	(%)
	Area of FMU	**15460**	100	**12909**	100	**10474**	100	**38844**	100
Forest	Spruce-fir stands	11341	73.4	7524	58.3	7395	70.6	26261	67.6
	Deciduous stands	920	5.9	369	2.9	337	3.2	1625	4.2
	Jack pine stands	305	2.0	584	4.5	49	0.5	938	2.4
	Lichen woodland	19	0.1	163	1.3	502	4.8	684	1.8
	sum of forested areas	12585	81.4	8640	66.9	8283	79.1	29507	76.0
Non-Forest	Water	2106	13.6	2510	19.4	1129	10.8	5745	14.8
	Wetlands	234	1.5	597	4.6	225	2.2	1057	2.7
	Lichen heaths	191	1.2	671	5.2	578	5.5	1439	3.7
	Heaths without lichen	281	1.8	454	3.5	236	2.3	971	2.5
	Other	63	0.4	37	0.3	23	0.2	124	0.3
	sum of non-forested areas	2875	18.6	4269	33.1	2191	20.9	9336	24.0
Disturbances	Fire < 10 years old	7	0.0	245	1.9	20	0.2	272	0.7
	Fire < 20 years old	314	2.0	722	5.6	20	0.2	1057	2.7
	Fire < 40 years old	505	3.3	2487	19.3	117	1.1	3108	8.0
	Fire < 60 years old	511	3.3	2639	20.4	151	1.4	3301	8.5
	Logging < 10 years old	791	5.1	263	2.0	230	2.2	1285	3.3
	Logging < 20 years old	2103	13.6	509	3.9	741	7.1	3353	8.6
	Logging < 40 years old	3358	21.7	509	3.9	751	7.2	4619	11.9
	Logging < 60 years old	3740	24.2	514	4.0	757	7.2	5011	12.9
	Road density (km/km^2)	0.92	-	0.14	-	0.27	-	0.48	-
Land allocation	IUCN protected areas	218	**1.4**	424	**3.3**	482	**4.6**	1124	**2.9**
	Caribou protection blocks	1220	**7.9**	1036	**8.0**	2202	**21.0**	4458	**11.5**
	Non-protected areas	14022	90.7	11450	88.7	7791	74.4	33263	85.6
	Operable productive areas	11147	72.1	7180	55.6	5599	53.5	23925	61.6
Level of timber supply (m^3/year)		856024		434400		372600		1663024	

Paper birch (*Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michaux) are found as companion species or in pure stands following recent disturbance. Non-forested areas cover 24% of the study region and are dominated by water bodies (14.8%), lichen heaths (3.7%), wetlands (2.7%), and heaths without lichen (2.5%) (Table 3.1). The two main disturbance regimes occurring into the study region are fire and forest harvest. The latest spruce budworm (*Choristoneura fumiferana* (Clemens, 1865)) outbreaks occurred between 1974 and 1985 in the south of our study region (Bouchard *et al.* 2008a) and the frequency of windthrows is considered low in comparison with fires and logging (Bouchard *et al.* 2009). The fire regime in the study region has been extensively studied using historical fire maps from 1800 to 2000 (Bouchard *et al.* 2008a). Mean fire return interval for the study region is estimated at 270 years [95% CI: 234 - 310] (Bouchard *et al.* 2008a) and the empirical fire size distribution is known for the last 200 years (Bouchard *et al.* 2008b). Industrial forestry (clearcutting system) in the region started during the second half of the 20th century with increasing availability of mechanization and the development of the road network. Logging activities started in the southern part of the region and has since extended northwards. This process yielded a north-south gradient in logging intensity with older logging in the south and more recent logging in the north. Logging activities are organized according to administrative units called forest management units (FMUs) (see Fig. 3.1). For each FMU, a planned timber supply is calculated by provincial authorities to provide the amount of timber volume that can be harvested annually by forest companies. Each forest company is responsible for harvesting operations and wood transportation, from logging areas to their mill.

Conservation scenarios

Permanent protected areas (hereafter named "IUCN protected areas") belong to categories Ia and III such as defined by IUCN and their size ranges from 275 ha to 48240 ha. Their cumulative area represented less than 3% of the study area (Table 3.1, Fig. 3.2B). Caribou protection blocks are part of the recovery strategy of boreal caribou in Québec (Courtois *et al.* 2004; Équipe de rétablissement du caribou forestier au Québec 2008) and their cumulated areas represented ~12% of the study area, while their proportion varies among FMUs (Table 3.1, Fig. 3.2C). Their mean size is ~10000 ha (± SD = 13000 ha; Minimum ≈

100 ha; Maximum ≈ 63000 ha). Caribou protection blocks in the recovery strategy are aimed to be temporary and floating reserves in space and time. However, their effective duration in practice and the spatial location in the future are unknown (S. Heppel, MRNF, Pers. Comm.). Consequently, we considered that caribou protection blocks were permanent. We distinguished three different conservation scenarios that varied as a function of the amount of conservation areas (Fig. 3.2). In *scenario 1*: mature productive forests could be logged, irrespective of the delineation of caribou protection blocks or IUCN protected areas. In *scenario 2*: logging happened everywhere in mature productive forests but only outside IUCN protected areas. In *scenario 3*: logging had to be located in productive forests located outside IUCN protected areas and caribou protection blocks.
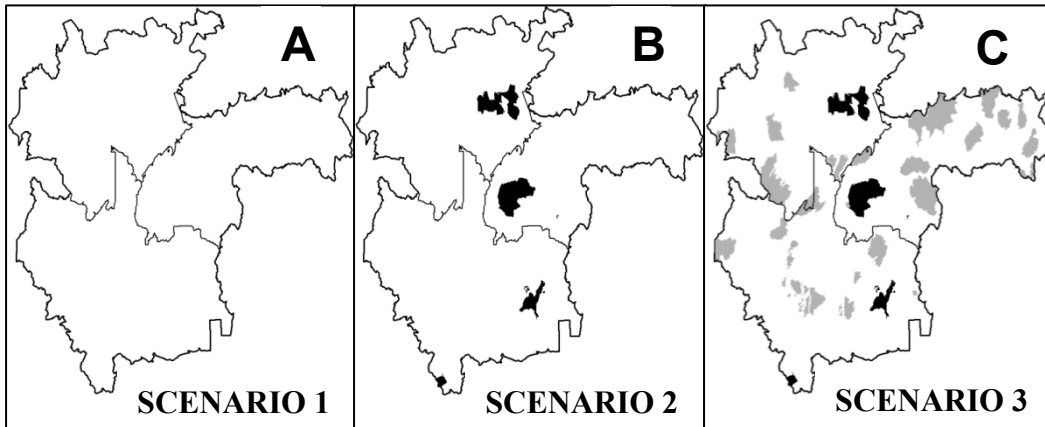
Figure 3.2. Spatial representation of the three conservation scenarios tested in this study: A) scenario 1 or control with no conservation areas; B) scenario 2 with only IUCN protected areas (in black); and C) scenario 3, the scenario currently applied on the ground, with IUCN protected areas (in black) and caribou protected blocks (in gray). Forest harvesting is forbidden within IUCN protected areas and caribou protected blocks.

Simulation experiment

We used the latest forest inventory data (MRNFQ 2003), updated in 2010, to map information on forested and non-forested areas, disturbance (logging and fire) history, and road network. The smallest polygons of forest inventory maps were ~8 ha. Delineations of FMUs, permanent protected areas and caribou protection blocks were provided by the Ministère des ressources naturelles et de la faune du Québec (MRNFQ). All maps were rasterized to a 200 m x 200 m pixel size prior to be used in our simulation experiment. We

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used the Spatially Explicit Landscape Event Simulator (SELES; Fall & Fall, 2001) to investigate how increasing conservation areas under multiple disturbance regimes influenced boreal caribou population dynamics and economic indicators important for forest industry. Simulation modelling has been successfully used in the past to better understand spatiotemporal interactions among multiple disturbance regimes on boreal forest dynamics (Fall et al. 2004, Didion et al. 2006, James et al. 2007, James et al. 2011) and their interaction effects with conservation planning (Rayfield et al. 2008, Côté et al. 2008, Tittler et al. 2012). For economic indicators, we calculated the amount of wood volume harvested annually, transportation costs and the amount of roads built. For each conservation scenario, we modelled three forest management scenarios based on different disturbance regimes. The first forest management scenario ignored wildfires and mirrored a management strategy where fire suppression would be 100% efficient. This scenario shares many similarities with the reference scenario of the Chief Forester Office of Québec that was used to calculate the level of timber supply used in this study, in every FMU, for the period 2008-2013. The second scenario accounted for both logging and fire but logging was constrained to undisturbed stands only (no salvage logging). The third scenario is closely related to what really happens in the field, namely that both fire and logging occur simultaneously, together with salvage logging when conditions are suitable. All together, the nine combinations of conservation and forest management scenarios in each FMU covered a wide assortment of conditions ranging from low proportion of conservation areas together with low disturbances rates to high proportion of conservation areas with high disturbances rates. We initialized the simulations with the latest available maps of the study region (i.e. 2010). Each scenario was run for one hundred and fifty years with an annual time step. We conducted explanatory analyses and performed 100 replicates of each scenario, which appeared to provide stable estimates of indicators.

Model description

For every scenario, we evaluated the annual population growth rate ($\lambda_{caribou}$) of boreal caribou, the amount of realized harvest level, and timber transportation costs. To do so, we simulated several dynamic processes including forest growth and aging, fire regime, logging regime, road construction, transportation costs, and $\lambda_{caribou}$ (see Fig. 3.3)
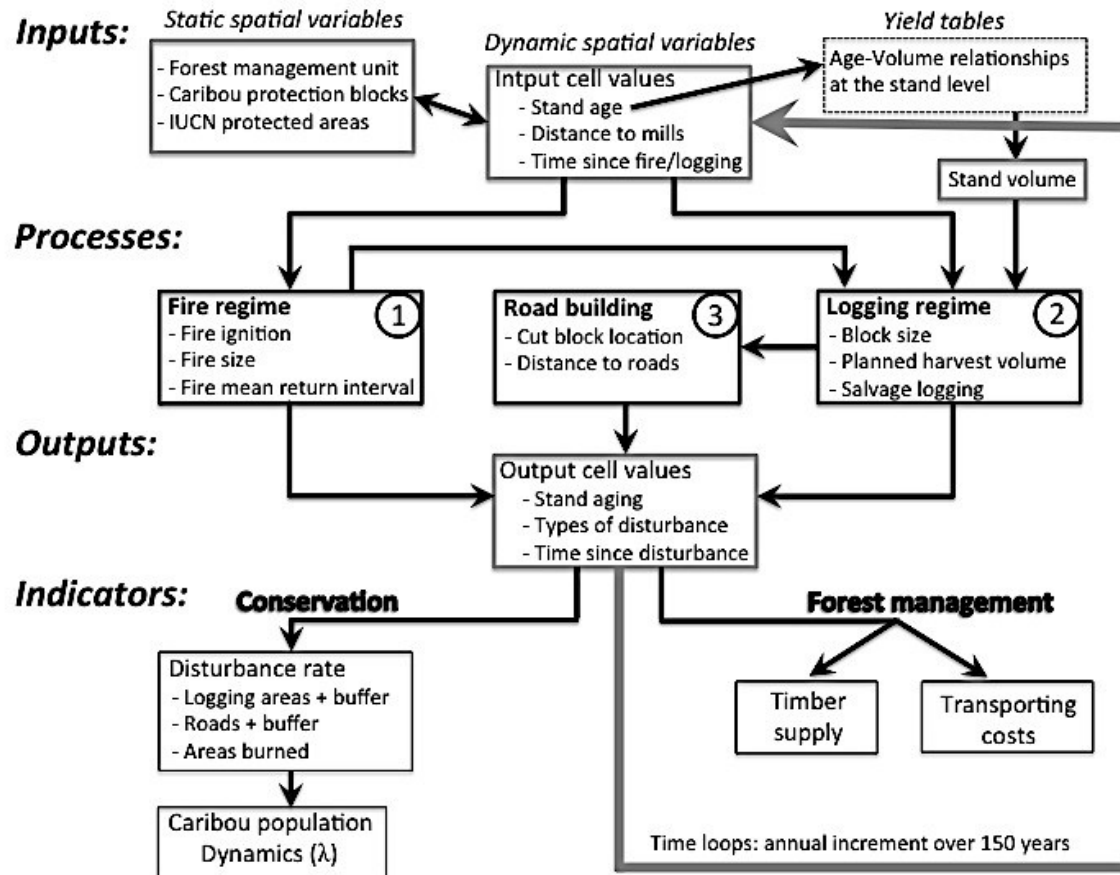
Figure 3.3. Diagram showing the main steps of our simulation model with inputs, processes, outputs and indicators. Box and arrows indicate how each element interrelate with each other in space and time. Inputs are composed of static spatial variables (i.e., values do not change in time and space), dynamic spatial variables (i.e., values change in time and space with porcesses) and stand yield tables. Processes involve three spatiotemporal sub-models: fire regime, logging regime and road building (see text for further details). Outputs are the results of actions caused by processes on input data and are spatially updated at each time step. Indicators track the changes in output maps at each time step that are relevant from a conservation (i.e., population growth rate of boreal caribou populations: $\lambda_{caribou}$) and forest management (i.e., timber supply and transportation costs) perspectives.

Forest Growth & Yield sub-model

We classified forest stands into four different species groups based on their composition, abiotic conditions, growth profile, tolerance to light and successional status as: 1) shade tolerant conifers (black spruce and balsam fir), shade intolerant conifer (Jack pine), mixed/deciduous species (aspens and white birch), and woodland lichen (Table 3.1). For each species group, we used yield curve predicting stand volume of coniferous species as a function of age. These yield curves were estimated as area-based weighted averages from yield tables calculated by the Chief Forest office for the last timber supply analysis of 2008-2013, following the model of Pothier & Savard (1998). Due to gradients in productivity over the study region, we divided the total area into 40 squares of ~10^3 km^2 each and calculated specific yield curves for each species group in every 10^3 km^2 square, which yielded a total of 192 yield curves. Stand age was updated at each time step and we assumed that pixels experiencing a disturbance (fire or logging, see below) remained in their initial species group.

Fire sub-model

To simulate fires over the study region, we used a modified version of the fire stochastic dynamic model of Bouchard & Pothier (2008b) that has been previously calibrated for the same study area. This fire model is a percolation model with three main stochastic components: the number of fire that starts each year, the initial location point where each fire starts (= ignition point), and the size of each fire. Fires smaller than 10 km^2 were not considered in this study because reliable long term data were not available and because they contribute little to the total area burned (Bouchard & Pothier 2008b). The annual number of fires was simulated using the following Poisson process:

$$N_{fire} \sim \text{Poisson}(\lambda_{fire}), \tag{1}$$

where λ_{fire} is the mean number of fire > 10 km^2 that ignite each year (see Table 3.2). Using iterative simulation and a mean fire interval of 300 years, we estimated $\lambda_{fire} = 0.86$ (Table 3.2). The spatial location of each fire ignition was the result of a random draw among pixels covered by forest or wetland. Each pixel that was classified either as forest or

wetland was assigned an equal probability of ignition. Otherwise, ignition probability was zero. We prevented fires from starting within 1200 m of water bodies to avoid that soon after ignition fire spreading stopped suddenly because of the proximity of water bodies. Once ignition started, each fire i was randomly assigned a size picked from the following reverse Weibull distribution:

$$Size_i \sim ReverseWeibull(shape, scale), \tag{2}$$

where shape and scale parameters were taken from Bouchard & Pothier (2008b) (see Table 3.2). To prevent unrealistic high fire sizes, maximum fire size was truncated to 2130 km^2, which corresponds to the biggest fire size observed in our study since 1800. Fire spreading was assumed to be independent of stand and site characteristics and we modelled it as a percolation model with equal probability of spreading in all cardinal directions. Due to a lack of any available indication showing the contrary, fire ignition and spreading were independent of administrative units (e.g., FMU or conservation areas).

Modelling fires randomly and independently for each scenario, at each year, and for each replicate led to extreme heterogeneity of fire pattern (Fig. 3.4). Even with 100 replicates, we could not guarantee that observed differences between scenarios were the direct result of variation due to scenarios (e.g. conservation areas, logging and road patterns) or of the heterogeneity in fire pattern between scenarios. To minimize the impact of this confounding effect, we used for each replicate common random numbers to ensure that for each year within each replicate, fire patterns were identical across scenarios.

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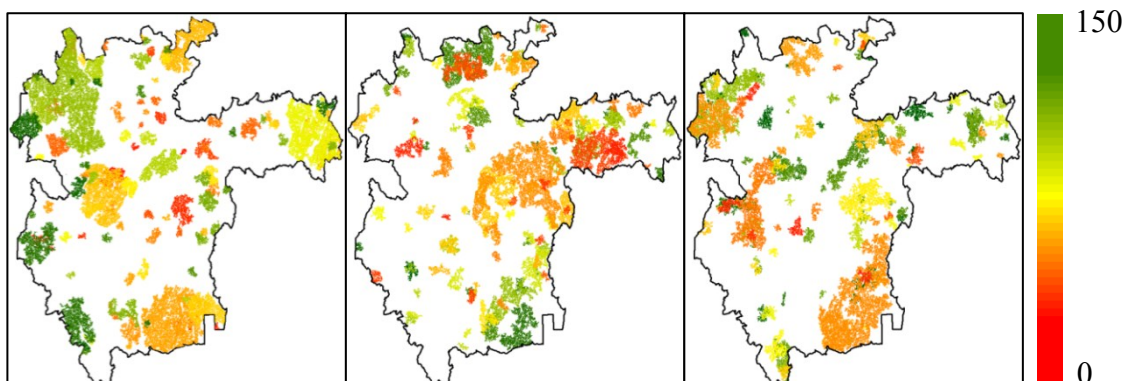
Figure 3.4. Three different simulated fire patterns obtained with our fire model after 150 years of simulation. Each figure represents a different simulation run where oldest simulated fires were coloured in green and most recent simulated fires were coloured in red.

Logging sub-model

The size of cut blocks was randomly distributed following a uniform distribution (see Table 3.2). We made a distinction between logging of undisturbed stands and salvage logging as these processes respond to different rules in forest management plans. For undisturbed stands, we took into account the following variables for a logging to occur: 1) stand age had to be older than a minimum harvesting age (Table 3.2); 2) older stands were harvested first; 3) stands located at shorter distance to roads were given priority over stands located further away; and 4) stands located at a shorter distance to mills were logged in priority. This set of rules was aimed at mirroring several constraints related to logging operations. Other rules could have been added but we limited the number of constraints to keep a balance between complexity and generality. These rules were translated into probabilities and combined to give a harvest probability surface at each time step. Thus, the actual location of cut blocks in a given year within each FMU is determined by a series of stochastic draws that is compared to this harvest probability surface.

For salvage logging, we retained two main variables: 1) the distance to the closest road; and 2) the amount of salvageable volume. Small fires located far from roads are not profitable for salvage logging because of low returns and excessive costs that are generated due to the amount of new roads to build and increasing distances for transporting wood.

Table 3.2. Parameters of the different sub-models used in our simulation spatial experiment.

Sub-model	Variables	Probability Distribution	Parameter(s)	References
YIELD	Yield tables	fixed	-	Pothier & Savard (1998)
FIRE	Mean number of fire per year	Poisson(λ_{fire})	λ_{fire} = 0.86	Adapted from Bouchard & Pothier (2008b)
	Fire size	Reverse Weibull(shape, scale)	shape = 0.7357	Bouchard & Pothier (2008b)
			scale = 0.0386	Bouchard & Pothier (2008b)
LOGGING	Size of cut blocks (ha)	Uniform(min, max)	min = 50	RNI (2002)
			max = 150	RNI (2002)
	Planned harvest volume[1] (m^3/year) in FMU 1	fixed	856024 [2]	fixed by simulation
	Planned harvest volume (m^3/year) in FMU 2	fixed	434400	fixed by simulation
	Planned harvest volume (m^3/year) in FMU 3	fixed	372600 [3]	fixed by simulation
	Minimum stand age for logging (yrs)	fixed	90	Pothier & Savard (1998)
	Maximum distance to roads (km)	fixed	2	-
	Minimum volume for salvage logging (m^3/ha)	fixed	50	Produits Forestiers Résolus (Pers. Comm.)
CARIBOU	β_0 (see eqn 5 in Methods)	Normal($mean_{(0)}$, $sd_{(0)}$)	$mean_{(0)}$ = 44.265	Env. Can (2011)
			$sd_{(0)}$ = 2.942	Env. Can (2011)
	β_1 (see eqn 5 in Methods)	Normal($mean_{(1)}$, $sd_{(1)}$)	$mean_{(1)}$ = -0.429	Env. Can (2011)
			$sd_{(1)}$ = 0.061	Env. Can (2011)
	Standard deviation of recruitment rate	fixed	0.049	Courtois et al. (2003)
	Survival rate	Normal(mean, sd)	0.85	Env. Can (2011)
			0.0525	Courtois et al. (2003)
COSTS	mean cost per cubic meter (m^3x km)	fixed	17.6	Adapted from Moore et al. (2011)

[1] Values of planned harvest volume are for commercial coniferous species: balsam fir, spruce, Jack pine, larch.
[2] Planned volume has been rescaled proportionally to the area removed in the southern part of the FMU 1 (see Methods).
[3] Planned volume has been lowered by 30% compared to the official value (see Methods).

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We accounted for this trade-off in simulating salvage logging only when the total amount of salvage volume by fire (m³) was ten times higher that Euclidian distance (in meters) between the ignition point and the closest road. This rule prevented salvage logging from occurring far from roads when available salvage volume was low. The maximum standing salvage volume available for harvest in a given year in each pixel was thirty percent of the volume prior to the fire event (J. Duval, MRNF, *Pers. comm.*) and a minimum of 50 m³/ha was required for a salvage logging to occur (J. Duval, MRNF, *Pers. comm.*). When a fire occurred and conditions for salvage logging were satisfied, salvage logging were given a higher priority (probability) over standard logging because of the emergency of harvesting burned volumes to avoid fast degradation of wood by insects (Nappi *et al.* 2004). Once a burned area was salvaged, it was then reclassified as a logged area (see Caribou sub-model below).

To quantify the impact of fire and conservation zones on the level of timber harvest, we defined levels of timber harvest in each FMU based on the control scenario without fire and conservation zones. The level of timber harvest was calculated by iteration separately for each FMU, so that shortfalls in timber harvest volume over a period of 150 years did not exceed 5% of the total amount of volume harvested over the same period of time.

Road Building sub-model

Spatial configuration of the road network plays a fundamental role both in forest operations (e.g. transportation costs) and on boreal caribou (Fortin *et al.* 2013). The main road developments in the study region are related to logging activities (accessibility of machinery, timber extraction, and transport). Therefore, our spatial dynamic model of road development was closely related to logging activities (see above). Each time a cut block was located further than 500 meters from the nearest road (maximum skidding distance), a new road was built using the Euclidean distance to connect the centroid of the new cut block to the nearest existing road. As cut blocks are more likely to occur at a low distance from roads, this rule emulates the known pattern of progressive south to north logging intensity and road density.

Transportation Cost sub-model

Costs of timber transport directly depend on the spatial configuration of the road network, the location of mills and spatial distribution of mature forests. Transportation costs are thus the main source of cost that is likely to be influenced by changes in spatial constraints imposed by different conservation schemes. Transportation costs depend on many variables among which two are essential: 1) the distance from harvested areas to mills; and 2) the amount and the size of timber that are transported. To calculate the distance between logged areas and mills, we evaluated the least cost path of each pixel to the closest mill given the road network. In combining values of least cost path with values of distance to roads, we were able to calculate for each pixel the minimum distance between pixel location and the final destination of timber logs. The map of least cost path was updated at each time step along with maps of road network and distance to roads. The second variable, the amount and the size of timber that are transported, depends on the type of silvicultural treatment applied (Liu *et al.* 2007). Moore *et al.* (2012) showed in the same study region that for a clearcutting system similar to the one simulated here, the mean cost per cubic meter associated to transport is \$17.6 m^{-3}, or about 40% of the total of timber supply costs. In their study, the mean distance from logging areas to mills in their sectors was ~200 km, so in order to get a cost value by kilometer, we estimated the cost per cubic meter and per kilometer associated to transport as \$17.6/200 = \$0.085 m^{-3} km^{-1}. We estimated the transportation cost associated to each simulated cut block in our study by multiplying the *per unit* cost of transport by the volume harvested in cubic meter and by the least cost distance from the cut block to the mill (as above) as:

$$\text{Transportation cost (CAN\$)} = 0.085 \ (\text{CAN\$ } m^{-3} \ km^{-1}) \times \text{least cost distance (km)} \times$$
$$\text{volume harvested } (m^3) \qquad\qquad (3)$$

Annual transportation costs were obtained by summing transportation costs associated to every cut block harvested each year.

Caribou Population Dynamic sub-model

Following Hatter and Bergerud (1991) and assuming that immigration and emigration compensate each other, the annual population growth rate (λ) can be expressed as a function of the annual adult mortality rate (M) and the annual recruitment rate (R):

$$\lambda = (1\text{-}M) / (1\text{-}R). \tag{4}$$

In a Canada-wide analysis across a sample of 24 boreal caribou population ranges, Environment Canada (2011) found that 69% of the variation in calf recruitment rate (the number of calf by 100 adult females) was explained by the percent of total disturbance on each range, according to the following linear relationship:

$$\text{Mean recruitment rate} = \beta_0 + \beta_1 \text{ x total disturbance} + \varepsilon \tag{5}$$

Where $\hat{\beta}_0 = 44.265 \pm 2.942$ and $\hat{\beta}_1 = -0.429 \pm 0.061$ (Environment Canada 2011). Here, total disturbance refers to burned areas + logged areas with a buffer of 500 m + roads with a buffer of 500 m. All these variables were outputs of the fire, logging and road models described above. For the calculation of equation 5, a pixel was classified as disturbed (fire or logging) if a diturbance occurred during the last 40 years.

In the recruitment-disturbance relationship, population range was defined as the geographic area occupied by a group of individuals that are subjected to the same influences affecting vital rates over a defined time frame. In our study region, however, there is no evidence of discrete boreal caribou populations and geographic delineation of population ranges remains unidentified. Therefore, we retained the delineation of FMU to assess demographic parameters. Rationales for this choice were as follows: 1) the area of each FMU is greater than the minimum area (10^4 km^2) recommended for evaluating demographic parameters for boreal caribou (Courtois *et al.* 2004; Environment Canada 2008); 2) previous estimations of demographic parameters around our study region were made within three main study areas (see Courtois *et al.* 2007). One of these areas (Manicouagan) fully encompassed our study region and overlapped, at more than 85%, FMU 1; and 3) boreal caribou occurs within every FMU.

To include parameter uncertainty as a source of stochasticity in our model, we drew normal random variables for $\hat{\beta}_0$, $\hat{\beta}_1$, recruitment rate and survival rate in our model. Specifically, $\hat{\beta}_0 \sim$ Normal(mean$_{(0)}$, standard deviation$_{(0)}$) and $\hat{\beta}_1 \sim$ Normal(mean$_{(1)}$, standard deviation$_{(1)}$), recruitment rate $\sim$ Normal(mean recruitment, standard deviation recruitment) and survival rate $\sim$ Normal(mean survival, standard deviation survival), where the mean recruitment was obtained in equation 5 and all other parameters were estimated from the literature (see Table 3.2).

Using equation 4, we then estimated $\lambda_{caribou}$ for each FMU at each time step of each scenario. We calculated for each year and for each FMU, the probability that $\lambda_{caribou} > 1$ (Prob$_{\lambda>1}$) as the number of replicates where $\lambda_{caribou} > 1$ divided by 100, the total number of replicates. If Prob$_{\lambda>1}$ was higher than 0.6, the risk that each FMU cannot support a self-sustaining caribou population was from low to very low, if $0.4 <$ Prob$_{\lambda>1} < 0.6$, the risk was intermediate and if Prob$_{\lambda>1} < 0.4$, the risk was from high to very high (Environment Canada 2012).

Results

Caribou population dynamics

Initial landscape characteristics differed among forest management units (FMUs) in the percentage of burned and logged areas, the amount of productive forests, and the percentage of caribou protection blocks (Table 3.1). At the beginning of simulations, the probability that $\lambda>1$ (hereafter Prob$_{\lambda>1}$) was 30% lower in FMU 1 than in FMUs 2 and 3, highlighting the higher proportion of anthropogenic disturbances in the southern part of the study region (Figs 3.4 A-I).

The response of Prob$_{\lambda>1}$ over time differed markedly in every FMU as a function of the different scenarios of conservation and forest management (Figs 3.4 A-I). In FMU 1, increasing conservation areas from 0 (scenario 1) to 7.9 % (scenario 3) had no impact on Prob$_{\lambda>1}$ whenever fire or salvage logging were taken into account or not (Figs 3.4 A-I). Prob$_{\lambda>1}$ decreased almost linearly from 1 to 65 years and by year 40-45, the level of risk that population range is not self-sustaining became high (Prob$_{\lambda>1} < 0.4$; see Environment

Canada 2012) and remained so until year 150. In FMUs 2 and 3, values of $Prob_{\lambda>1}$ were not influenced by the presence or absence of IUCN protected areas alone (scenarios 1-2, Figs 3.4 D-I).

However, the inclusion of caribou protecting blocks together with IUCN protected areas (scenario 3) in FMUs 2 and 3 allowed, in one hand, to reduce by 5 to 20% the decreasing rate of $Prob_{\lambda>1}$ over time and, on the other hand, to decrease the minimum values of $Prob_{\lambda>1}$ by 10 to 40% compared to scenarios 1-2 (Figs 3.4 A-C vs D-I). Hence, low values of $Prob_{\lambda>1}$ happened later on and lowest values of $Prob_{\lambda>1}$ were much higher in scenario 3 than in scenarios 1-2 within these FMUs. These differences in $Prob_{\lambda>1}$ between scenario 3 and scenarios 1-2 were directly related to the type of forest management.

In absence of salvage logging, the level of risk that population range was not self-sustaining ranged from very low to moderate in scenario 3 (Figs 3.5B and 3.5C) compared to scenarios 1-2 where it ranged from very low to high (Figs 3.5E, 3.5F, 3.5H, 3.5I). In presence of salvage logging, the risk that population range was not self-sustaining ranged from very low to moderate in FMU 3 in scenario 3 (Fig. 3.5A) whereas it ranged from very low to high in conservation scenarios 1 and 2 (Figs. 3.5D, 3.5G).
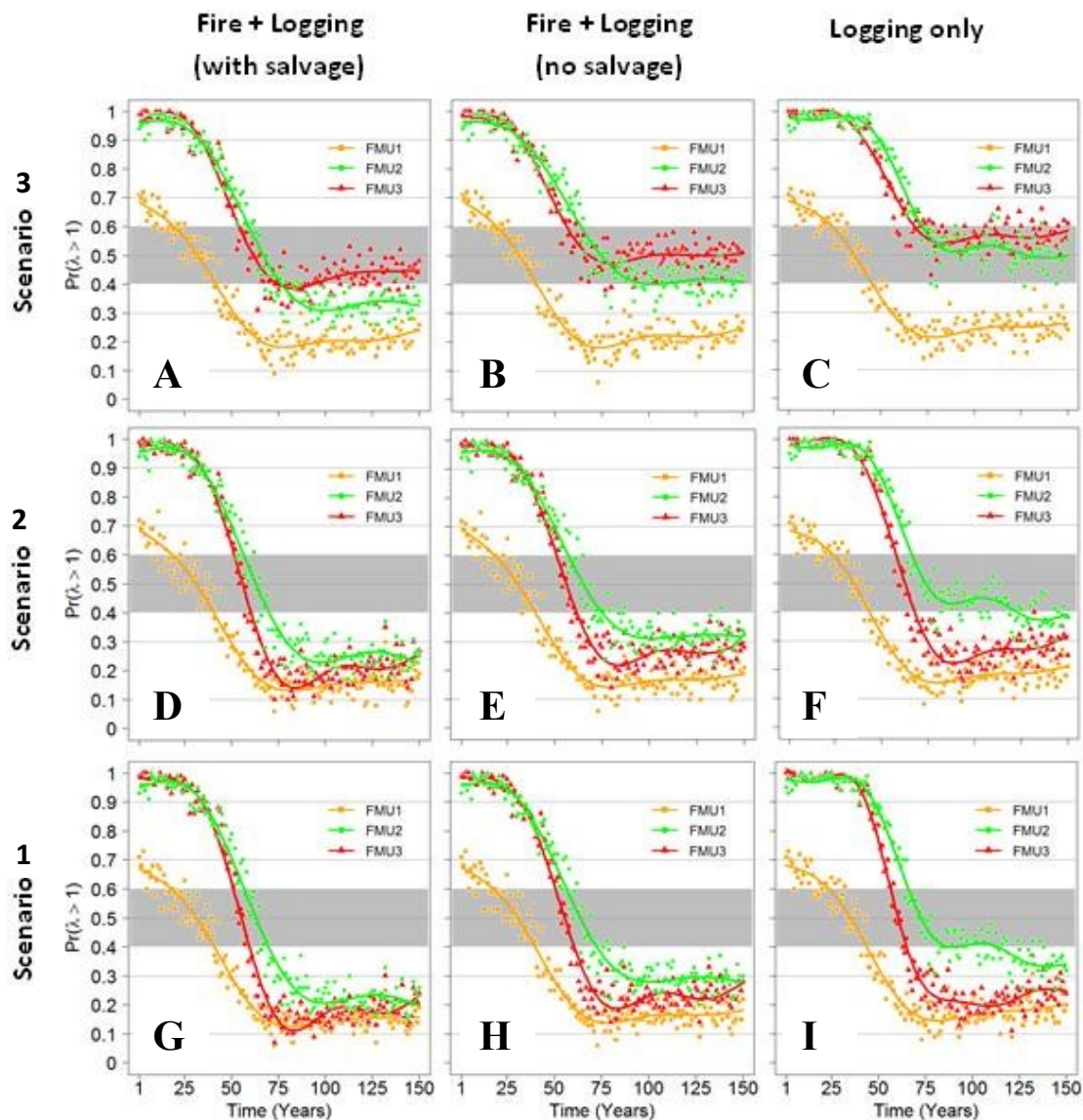
Figure 3.5. Relationship between Pr(λ>1) (i.e. the probability that population growth rate of boreal caribou > 1) and simulation time (year 1 = 2010) for each forest management unit (FMU 1 in orange, FMU 2 in green, and FMU 3 in red) as a function of scenario type for conservation (upper y-axis: scenario 1, 2 or 3) and forest management (upper x-axis). Each letter refers to a unique combination of conservation and management scenario and each data point was calculated from 100 independent replicates using our spatial simulation experiment (see methods). Solid lines are cubic splines fitted to the data.

Realized vs planned harvest volume

From a timber supply perspective, we found that increasing conservation areas negatively impacted the level of realized harvested volume but that the magnitude of these impacts depended on the type of forest management and FMUs. Increasing conservation areas in FMUs 2 and 3, when wildfires were absent, yielded critical periods for which 100% of simulations showed reductions greater than 10% of the realized harvest volume, compared to what was initially planned (Figs 3.6C and 3.6F).
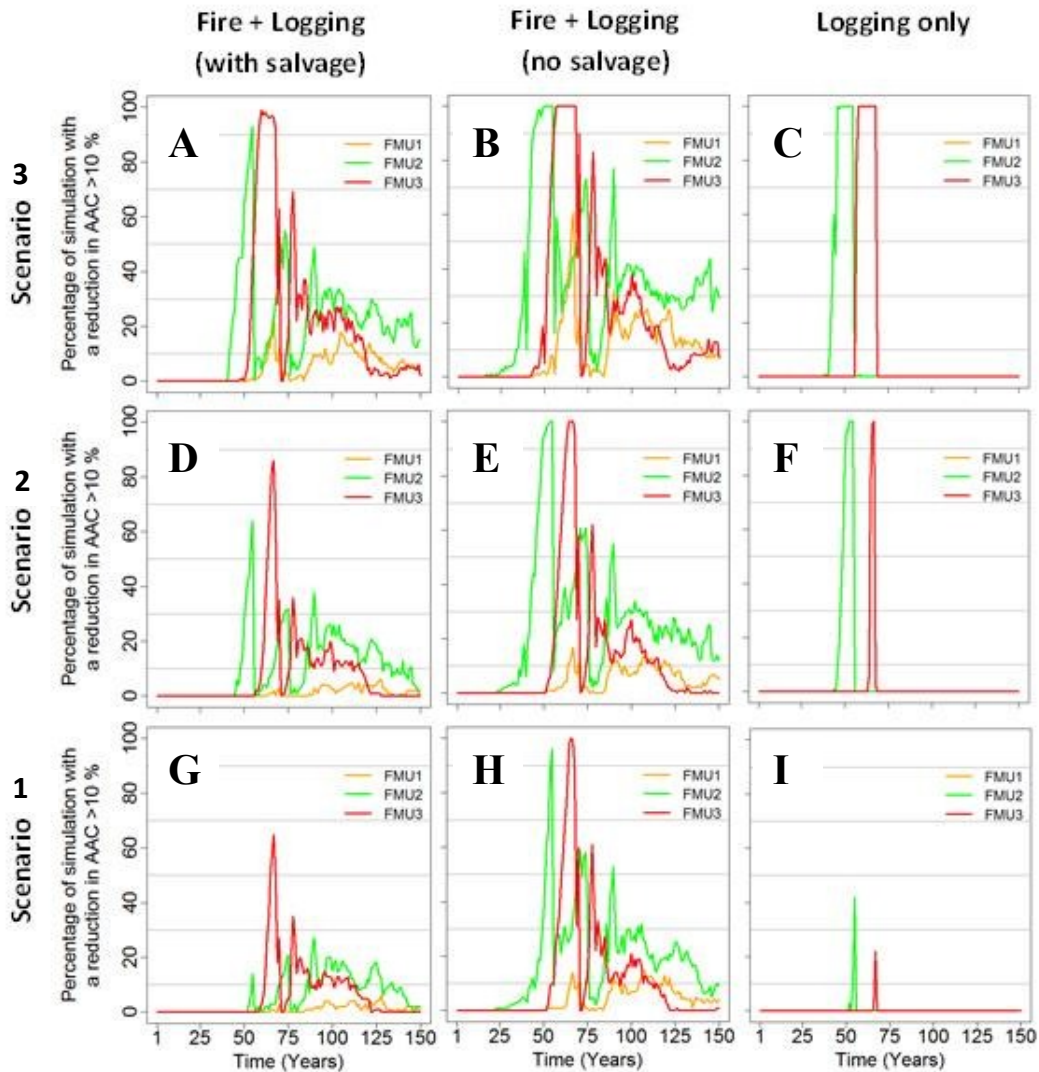
Figure 3.6. Relationship between the percentage of simulation that did not reach the level of planned harvest volume (=allowable annual cut or AAC) and simulation time for each forest management unit (FMU 1 in orange, FMU 2 in green, and FMU 3 in red) as a function of scenario type for conservation (upper y-axis: scenario 1, 2 or 3) and forest management (upper x-axis). Each data point was calculated from 100 independent replicates using our spatial simulation experiment (see methods).

But, we failed to detect any impact of increasing conservation areas on the realized harvest volume for FMU 1 (Figs 3.6C, 3.6F, 3.6I). In presence of fire but in absence of salvage logging, FMUs 2 and 3 experienced several critical periods of important reduction in the amount of realized harvest volume, even in absence of any conservation measure (Fig. 3.6H). Increasing conservation areas in such management scenario caused important failures in the level of volume harvested in all FMUs: critical periods of reduction in realized harvest volume happened more often, sooner in time and lasted longer (Figs 3.5B, 5E, 5H). In presence of fire, salvage logging allowed reducing the gap between the levels of realized *vs* planned harvest volume under every conservation scenario (Figs 3.6A, 3.6D, 3.6F vs 3.6B, 3.6E, 3.6H), but especially in FMU 1. For FMUs 2 and 3, however, salvage logging could not prevent the occurrence of critical periods with important reduction in the level of realized harvest volume once IUCN protected areas or caribou protection blocks were taken into account (Figs 3.6A, 3.6D).

Transportation Costs and the amount of roads built (km)

We recorded both annual transportation costs in each FMU and the amount of roads built annually in the entire study region, for each of the first 35 years of each simulation run. This time period allowed us to make reliable comparisons among scenarios as the realized and planned harvest volumes were equal in all scenarios and in all FMUs (see Fig. 3.6). We found significant differences of transportation costs among conservation scenarios which confirmed our hypothesis that the spatial arrangement of conservation areas can induce specific additional costs other than opportunity costs related to the non-harvesting of timber volume inside conservation areas. Overall, we found that most of the magnitude in the difference of transportation costs among conservation scenarios was attributable to caribou protection blocks and not to IUCN protected areas, irrespective of the type of forest management. Indeed, the median difference of transportation costs between scenarios 1 and 2 was below 1% in all FMUs, irrespective of the presence or absence of fire and/or salvage logging (Figs 3.7A-C). Of all FMUs, FMU 3 had the highest proportion of caribou protection blocks and exhibited the highest median difference of transportation cost, from 6 to 10%, compared to the scenario of no conservation or IUCN protected areas only (Figs 3.7A-C). It is interesting to note that if the occurrence of fires slightly increased the

variation in transportation costs compared to a scenario with absence of fire (Figs 3.7B vs 3.7C), variability in transportation costs was multiplied by 3 when salvage logging was allowed to occur. Therefore, random variation in the spatial pattern of wildfire and salvage logging can induce up to 25% of additional transportation costs (the upper limit of 95% CI) which increase the uncertainty about the profitability of salvage logging (Fig. 3.7A). In the presence of fire and salvage logging, the spatial cost of caribou protection blocks and IUCN protected areas (Fig. 3.2C) is about 3% when compared to the scenario of no conservation area for the entire study area (Fig. 3.7A).
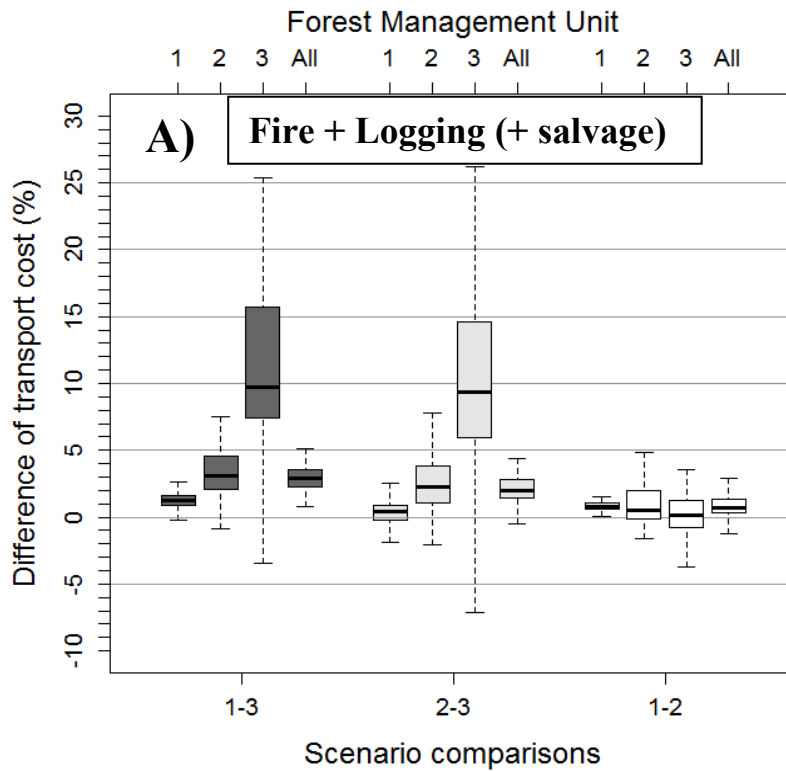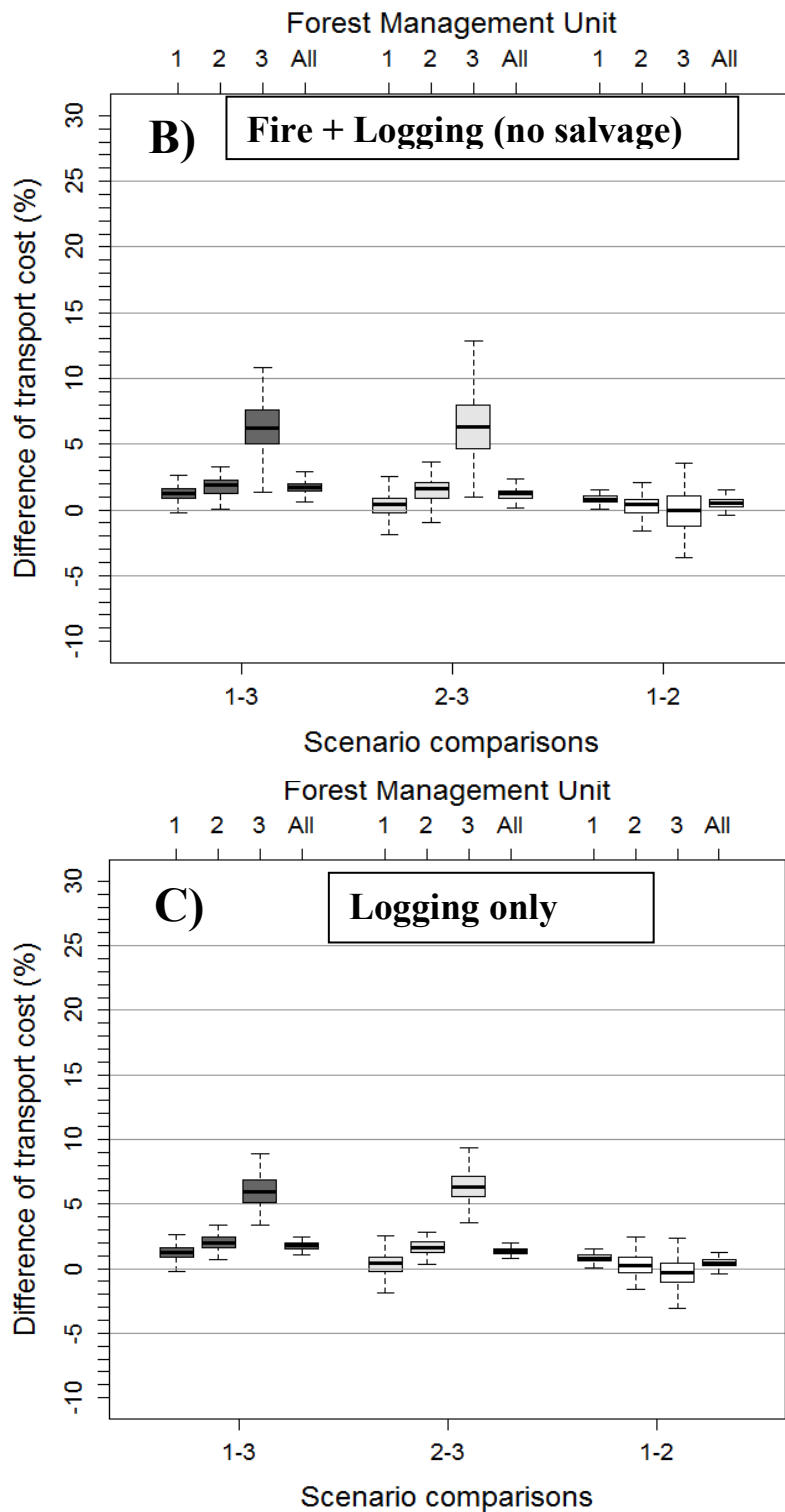
Figure 3.7. Boxplots representing differences of transportation costs among each pairwise comparison of conservation scenario (below x-axis) for each forest management unit (upper x-axis) in presence of A) Fire + logging (+ salvage logging); B) Fire + logging (no salvage logging); and C) Logging only. Transportation costs were estimated for each of the 100 replicates of every scenario as the sum of annual value over the first 35 years of simulation (see Result section).

In absence of salvage logging, caribou conservation blocks and IUCN protected areas together increased by ~6% the amount of road built after 35 years compared to the scenario of absence of conservation areas (Fig. 3.8). This increase mirrored spatial constraints imposed by the spatial arrangement of conservation areas given the development of the actual road network and the spatial distribution of mature stands. As for transportation costs, the occurrence of salvage logging increased by more than 75% the variability in the amount of roads built compared to scenarios without salvage logging (Fig. 3.8).
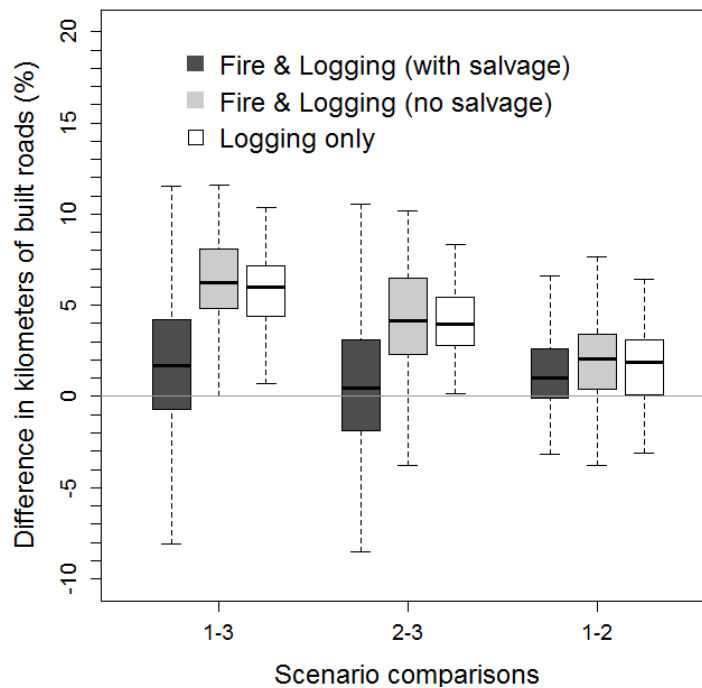
Figure 3.8. Boxplots representing differences in the amount of built roads (km) among each pairwise comparison of conservation scenario for every scenario of forest management. The amount of road built was estimated for each of the 100 replicates of every scenario as the sum of annual value over the first 35 years of simulation (see Result section).

Discussion

Competition for the same forest resources is an increasing source of conflict between industrial forestry and conservation planning worldwide. Fire also competes with harvesting of timber but the impacts of wildfires and salvage logging on possible trade-offs between economic and conservation objectives remain unknown. Our study showed that

fire increased conflicts between forest management and habitat conservation of boreal caribou in the eastern boreal forest of Canada. In presence of fire and caribou protection blocks, harvest levels planned without these constraints could neither provide a sustainable timber supply for the forest industry, nor ensure long term landscape suitability for boreal caribou persistence. Although an increase in the amount of caribou protection blocks improved the probability of a positive population growth rate of boreal caribou, the actual amount of caribou protection blocks was insufficient in all FMUs to compensate for high anthropogenic disturbance rates. These results are supported by several studies which showed that not considering explicitly the effects of fires (Savage *et al.* 2010), conservation areas (Leppänen *et al.* 2005) or spatial constraints in harvest schedule (Baskent & Keles 2005) in timber supply analyses overestimate the amount of planned volume available for harvest. Although we showed here that salvage logging helped to reduce the magnitude of the decline in the level of realized harvest volume, it could not prevent the occurrence of critical periods with important shortfalls in timber supply. Costs associated with salvage logging were also high and exhibited considerable variation which limits any economic benefits of salvage logging to areas located close to existing roads and mills. If we add to these limitations the ecological impacts of salvage logging on postfire communities and biodiversity (Schmiegelow *et al.* 2006, Lindenmayer & Noss 2006), the ability and desirability of using salvage logging as a planning tool to mitigate economic losses due to fire seems low. Salvage logging, however, might be an option in particular case for example when post-fire tree regeneration densities are critically low (Boiffin & Munson 2013). Overall, our results indicate that a policy that does not take into account explicitly the spatial constraints over time imposed by conservation areas and fire risk is unlikely to be sustainable for both boreal caribou conservation and timber supply.

If managers aim to simultaneously improve landscape suitability for boreal caribou populations and sustainable timber supply in the study region, a downward review of planned harvest levels that explicitly include constraints imposed by conservation areas and fire risk should be the first priority, especially in FMUs 2 and 3. The practical way this reduction is set up on the ground, however, will be a key element for identifying further trade-offs with minimal losses between caribou conservation and forest management. Our

results point out towards two main different planning strategies that deserve to be explored in the future. The first strategy relies on the current organization of forest management planning in three FMUs, as in this study, and applies lower levels of planned harvest volume in every FMU. With this strategy, however, the proportion of protection blocks for which boreal caribou populations are self-sustaining in the long term is unknown and will require further investigations under fire risk. For instance, we found that the negative impact of fires on the probability of observing a positive population growth rate increased in FMUs that had higher conservation areas. Hence, further levels of protection effort should account for this pattern and should, at a minimum, compensate for fire risk on the population growth rate. The second strategy might take advantage of the variation observed among FMUs in their response to the different conservation and forest management scenarios. FMU 1 had the best economic indicators and experienced the lowest rate of shortfalls in timber supply. This result likely mirrored the highest forest productivity, the lowest amount of conservation areas, and a well-developed road network in FMU 1 compared to the two other FMUs. FMU 1 also had the lowest probability to support a self-sustaining boreal caribou population because of the strength of legacies left by high historical rates of anthropogenic disturbance. In contrast, FMUs 2 and 3 showed the opposite trend with strong shortfalls in timber supply and high potential of boreal caribou populations to be self-sustainable. These variations in response of FMUs suggest that concentrating anthropogenic disturbances through zoning in areas of low conservation value, where forest productivity is the highest and transport costs the lowest should be an option to evaluate. Tittler *et al.* (2012) showed that concentrating intensive forest management on a small part of a boreal landscape may counterbalance losses associated with increasing protected areas at larger scale. Such zoning strategy applied at the FMU scale has the potential to bring similar economic benefits but in concentrating road construction, fragmentation, and habitat loss on particular FMUs. We therefore advocate for a thorough evaluation of concentrating forest harvest with lower planned harvest levels in FMU 1, together or not with intensive management, and to significantly lower forest harvest and road development in FMUs 2 and 3. This strategy will require that timber supply analysis be calculated for the study region as a whole instead of separately for each FMU. Variants between these two scenarios might include different sizes of caribou

protection blocks and cutblocks, as well as different spatial patterns of protected area network. Moreover, in the recovery strategy of boreal caribou in Québec (Équipe de rétablissement du caribou forestier au Québec 2008), caribou protection blocks are planned to be temporary (e.g. 60-100 years: Courtois *et al.* 2004) and their delineation can be dynamic in space and time. When the delineation of future protection blocks will be available, it will be then relevant to assess how dynamic reserves (Rayfield et al. 2008) influence population growth rate together with timber supply.

Finally, our results supported the hypothesis that spatial arrangement of conservation areas over the landscapes can increase the overall costs associated with timber log transportation. This result suggests that the spatial configuration of permanent protected areas and caribou protection blocks interact in space and time with other processes such as fire, forest harvesting, and road construction. These interactions likely impose additional spatial constraints on forest harvest planning which, in turn, influence transport-related costs. Over the study region, these additional "spatial" costs after the first 35 years of forest planning were 3% higher in the conservation scenario with permanent protected areas and caribou protection blocks than in the scenario with no conservation areas (scenario 1, Fig. 3.2A). Since these costs add to opportunity costs of timber volume that is set aside in conservation areas, it would be relevant to assess in the future how different spatial configurations of caribou protection blocks minimize this source of costs.

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References

Baskent, E. Z., & Keles, S. (2005) Spatial forest planning: A review. *Ecological Modelling*, **188**, 145-173.

Bearer, S., Linderman, M., Huang, J., An, L., He, G., & Liu, J. (2008) Effects of fuelwood collection and timber harvesting on giant panda habitat use. *Biological Conservation*, **141**, 385-393.

Bergeron, Y., Gauthier, S., Flannigan, M., & Kafka, V. (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology*, **85**, 1916-1932.

Bergeron, Y., Cyr, D., Drever, C. R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Le Goff, H., Lesieur, D. & Logan, K. (2006) Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. *Canadian Journal of Forest Research*, **36**, 2737-2744.

Boiffin, J. & Munson, A.D. 2013. Three large fire years threaten resilience of closed crown black spruce forests in eastern Canada. *Ecosphere* 4:art56.

Bouchard, M., Pothier, D., & Gauthier, S. (2008a) Fire return intervals and tree species succession in the North Shore region of eastern Quebec. *Canadian Journal of Forest Research*, **38**, 1621-1633.

Bouchard, M., & Pothier, D. (2008b) Simulations of the effects of changes in mean fire return intervals on balsam fir abundance, and implications for spruce budworm outbreaks. *Ecological Modelling*, **218**, 207-218.

Bouchard, M., Pothier, D., & Ruel, J. C. (2009) Stand-replacing windthrow in the boreal forests of eastern Quebec. *Canadian Journal of Forest Research*, **39**, 481-487.

Courtois, R., Ouellet, J. P., Dussault, C., & Gingras, A. (2004) Forest management guidelines for forest-dwelling caribou in Québec. *The Forestry Chronicle*, **80**, 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**, 491-498.

Didion, M., Fortin, M.-J. & Fall, A. 2007. Forest age structure as indicator of boreal forest sustainability under alternative management and fire regimes: A landscape level sensitivity analysis. *Ecological Modelling*, **200**, 45-58.

Environment Canada (2008) Scientific Review for the Identification of Critical Habitat for Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada. August 2008. Ottawa: Environment Canada. 72 pp. plus 180 pp Appendices.

Environment Canada (2011) Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices.

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 + 138pp.

Équipe de rétablissement du caribou forestier du Québec (2008) Plan de rétablissement du caribou forestier (*Rangifer tarandus*) au Québec − 2005-2012. Ministère des Ressources naturelles et de la Faune, Faune Québec, Direction de l'expertise sur la faune et des habitats, Canada. [In French.]

Fall, A., & Fall, J. (2001) A domain-specific language for models of landscape dynamics. *Ecological Modelling*, **141**, 1-18.

Fall, A., Fortin, M.-J., Kneeshaw, D.D., Yamasaki, S.H., Messier, C., Bouthillier, L. & Smyth, C. 2004. Consequence of various landscape-scale ecosystem management strategies and fire cycles on age- class structure and harvest in boreal forests. *Canadian Journal of Forest Research*, **34**, 310-322.

Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Gingras, C.T., Moorcroft, P.R., Courtois, R., & Dussault, C. (2013) Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. *The American Naturalist*, in press.

Government of Quebec (2010) Loi sur l'aménagement durable du territoire forestier. http://www2.publicationsduquebec.gouv.qc.ca/dynamicSearch/telecharge.php?type=2&file=/A_18_1/A18_1.html [Accessed on May 13, 2012].

Gutiérrez, R. J. (2008) Spotted owl research: a quarter century of contributions to Education, ornithology, ecology, and wildlife management. *The Condor*, **110**, 792-798.

Hatter, I. W., & Bergerud, W. A. (1991) Moose recruitment, adult mortality and rate of change. *Alces*, **27**, 65-73.

Hauer, G., Cumming, S., Schmiegelow, F., Adamowicz, W., Weber, M., & Jagodzinski, R. (2010). Tradeoffs between forestry resource and conservation values under alternate policy regimes: A spatial analysis of the western Canadian boreal plains. *Ecological Modelling*, **221**, 2590-2603.

James, P.M.A., Fortin, M.-J., Sturtevant, B.R., Fall, A. & Kneeshaw, D.D. 2011. Modelling spatial interactions among fire, spruce budworm, and logging in the boreal forest. *Ecosystems*, **14**, 60-75.

James, P.M.A., Fortin, M.-J., Fall, A., Kneeshaw, D.D. & Messier, C. 2007. The effects of spatial legacies following shifting management practices and fire on boreal forest age structure. *Ecosystems*, **10**, 1261-1277.

Leppänen, J., Linden, M., Uusivuori, J., & Pajuoja, H. (2005) The private cost and timber market implications of increasing strict forest conservation in Finland. *Forest policy and economics*, **7**, 71-83.

Lindenmayer, D. B., & Noss, R. F. (2006) Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology*, **20**, 949-958.

Liu, C., Ruel, J. C., & Zhang, S. Y. (2007) Immediate impacts of partial cutting strategies on stand characteristics and value. *Forest Ecology and Management*, **250**, 148-155.

Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-Being. Island Press, Washington, DC.

Ministère des ressources naturelles et de la Faune du Québec – MRNFQ (2003) Normes de cartographie écoforestière du troisième inventaire écoforestier. Forêt Québec. Direction des inventaires forestiers. ISBN 2-551-xxxxx-x. 109 p. [in French]

Moore, T. Y., Ruel, J. C., Lapointe, M. A., & Lussier, J. M. (2012) Evaluating the profitability of selection cuts in irregular boreal forests: an approach based on Monte Carlo simulations. *Forestry*, **85**, 63-77.

Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006) Integrating economic costs into conservation planning. *Trends in Ecology & Evolution*, **21**, 681-687.

Nappi, A., Drapeau, P., & Savard, J. P. (2004) Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? *The Forestry Chronicle*, **80**, 67-74.

Pothier, D. & Savard, F. (1998) Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources naturelles, Direction des inventaires forestiers. RN98-3054. [in French]

Rayfield, B.R., James, P.M.A., Fall, A. & Fortin. M.-J. 2007. Comparing static versus dynamic protected areas in dynamic boreal ecosystems. *Biological Conservation*, **141**, 428-449.

Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A. & Gutiérrez, R. J. (2012) Understanding and managing conservation conflicts. *Trends in Ecology & Evolution*, **28**, 100-109.

Roberge, J. M., Angelstam, P., & Villard, M. A. (2008) Specialised woodpeckers and naturalness in hemiboreal forests–Deriving quantitative targets for conservation planning. *Biological Conservation*, **141**, 997-1012.

Savage, D. W., Martell, D. L., & Wotton, B. M. (2010) Evaluation of two risk mitigation strategies for dealing with fire-related uncertainty in timber supply modelling. *Canadian Journal of Forest Research*, **40**, 1136-1154.

Schmiegelow, F. K., Stepnisky, D. P., Stambaugh, C. A., & Koivula, M. (2006) Reconciling Salvage Logging of Boreal Forests with a Natural-Disturbance Management Model. *Conservation Biology*, **20**, 971-983.

Schneider, R. R., Hauer, G., Adamowicz, W. L., & Boutin, S. (2010) Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biological Conservation*, **143**, 1603-1611.

Schneider, R. R., Hauer, G., Dawe, K., Adamowicz, W., & Boutin, S. (2012) Selection of Reserves for Woodland Caribou Using an Optimization Approach. *PloS One*, **7**, e31672.

Sorensen, T., McLoughlin, P. D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., & Boutin, S. (2008) Determining sustainable levels of cumulative effects for boreal caribou. *The Journal of Wildlife Management*, **72**, 900-905.

Tittler, R., Messier, C., & Fall, A. (2012) Concentrating anthropogenic disturbance to balance ecological and economic values: applications to forest management. *Ecological Applications*, **22**, 1268-1277.

Wilson, K. A., McBride, M. F., Bode, M., & Possingham, H. P. (2006) Prioritizing global conservation efforts. *Nature*, **440**, 337-340.

CONCLUSION GENERALE

Ma thèse s'inspire directement des principes de l'écologie des paysages pour quantifier l'importance des dimensions spatiales dans les relations entre le caribou forestier et la dynamique des paysages aménagés en forêt boréale. La contribution scientifique de cette thèse se décline selon trois principaux axes. Le premier axe est méthodologique et concerne la validation d'une approche statistique hiérarchique pour modéliser des données de distribution d'espèces spatialement auto-corrélées (chapitre 1). Le deuxième axe touche directement le domaine de l'écologie appliquée et vise à mieux comprendre les processus écologiques sous-jacents à la présence de gradients géographiques dans la sélection hivernale des paysages par le caribou forestier (chapitre 2). Finalement, le dernier axe aborde l'interface entre la conservation du caribou forestier en forêt boréale et la faisabilité des activités d'aménagement forestier, en présence d'un régime de feux (chapitre 3).

Modèles spatiaux de distribution d'espèces: INLA vs MCMC

Les modèles de distribution d'espèces sont couramment utilisés pour mieux comprendre comment les perturbations environnementales limitent la distribution des espèces (Elith & Leathwick 2009). Les prédictions dérivées de ce type de modèle servent notamment à évaluer l'effet des changements climatiques (Thuiller 2003) ou des stratégies de conservation (Cabeza et al. 2004) sur la distribution spatiale des espèces à statut précaire. Parmi la variété de modèles disponibles, les modèles hiérarchiques spatiaux se distinguent par un faible taux d'erreur de type I et II (Beale et al. 2010), ce qui en fait une méthode de premier choix pour modéliser des données de distribution d'espèces. Dans le premier chapitre, je montre que l'utilisation des approximations Laplace nichées et intégrées (*intergated nested Laplace approximations* - INLA; Rue et al. 2009) est une méthode aussi précise, mais bien plus rapide, que les simulations Markov Chain Monte Carlo (MCMC) pour calibrer des modèles statistiques hiérarchiques de distribution d'espèces à partir de données spatialement auto-corrélées. Le gain de rapidité et la précision d'INLA ouvrent de nouvelles perspectives dans la modélisation spatiale de données écologiques (Rue et al. 2009). Outre la capacité d'analyser des plus grands jeux de données, INLA permet désormais de réaliser dans un intervalle de temps raisonnable des analyses de sensibilité et

des validations croisées, ce qui améliore la transparence des modèles spatiaux bayésiens et évite de calibrer des modèles sur-paramétrés (*overfitting*). Concernant ce dernier point, ce chapitre contribue notamment à formaliser un cadre de modélisation qui balise la calibration de modèles spatiaux hiérarchiques (voir aussi Sørbye & Rue 2013). Il est désormais possible, d'un point de vue pratique en termes de temps et de ressources, d'évaluer rapidement le choix de différents *priors* sur l'estimation des paramètres pour ce type de modèle, ce qui constitue un progrès notable par rapport aux simulations MCMC.

INLA : perspectives et limitations

Dans ce premier chapitre, j'ai utilisé des modèles spatiaux statiques calibrés à partir de données surfaciques sur une grille régulière à faible résolution, ce qui est cohérent avec la résolution spatiale des normales climatiques. Toutefois, selon les objectifs de recherche et la disponibilité des données, il peut s'avérer important de caractériser l'influence de processus écologiques ayant une signature spatiale à plus petite échelle, comme c'est souvent le cas avec les interactions intra- et inter- spécifiques entre les organismes ou la dispersion. Des développements récents permettent aujourd'hui de calibrer rapidement une vaste gamme de modèles spatiaux hiérarchiques avec INLA à partir de données de localisations ponctuelles (*spatial point process models* – Illian et al. 2012, 2013). La disponibilité croissante de données à faible résolution spatiale, incluant les données GPS, rend ce type d'approche particulièrement attrayante et ouvre de nombreuses perspectives en écologie appliquée, notamment en ce qui concerne la calibration de modèles de distribution d'espèces à fine échelle spatiale (Renner & Warton 2013). Il est important de mentionner que comme toute méthode numérique, INLA a aussi des limitations. La principale limitation d'INLA pour modéliser des données de distribution d'espèces est l'incapacité actuelle de tenir compte explicitement de la détection imparfaite des espèces comme c'est le cas avec les modèles d'occupation des sites (*site occupancy models* – MacKenzie et al. 2002). La précision d'INLA diminue également lorsque le nombre d'hyper-paramètres (e.g. des paramètres contrôlant d'autres paramètres) augmente.

Expliquer les gradients géographiques dans la sélection des paysages par le caribou forestier.

Dans le deuxième chapitre de ma thèse, je montre en utilisant INLA que la distance par rapport aux routes explique mieux que les normales climatiques de température et de précipitation la présence de gradients géographiques dans la sélection hivernale des paysages par le caribou forestier au Québec. Ce résultat supporte l'idée qu'à moins d'un changement futur important des normales climatiques par rapport aux valeurs actuelles, les stratégies de conservation du caribou forestier au Québec devraient prioriser, à court et moyen termes, des mesures qui limitent directement l'étalement du réseau routier ainsi que la dégradation d'origine humaine de son habitat.

Il est toutefois important de noter que la disponibilité ainsi que la résolution spatiale et temporelle de données géospatiales pour un si grand territoire posent certaines limitations quant à l'évaluation de l'influence du climat sur la distribution du caribou forestier. Par exemple, l'inventaire des réseaux de pistes de caribou forestier a lieu uniquement durant la période hivernale. Il ne nous a donc pas été possible d'évaluer l'effet du climat à d'autres périodes de l'année, ce qui limite l'horizon temporel de nos inférences. Bien que les normales climatiques semblent avoir eu peu d'effets à l'échelle de notre zone d'étude, il est néanmoins possible que certains facteurs climatiques jouent un rôle sur la distribution spatiale du caribou forestier mais à une échelle couvrant de plus grands gradients longitudinaux et latitudinaux que ce que notre zone d'étude ne permettait de couvrir. D'autres études devront confirmer ou contredire cette hypothèse. Finalement, le manque de précision concernant les données de profondeur de neige à cette échelle ne nous a pas permis de tester précisément l'effet de cette variable.

Ces limitations ne nous permettent donc pas de conclure avec certitude que les changements climatiques n'auront pas d'influence sur la distribution spatiale du caribou forestier, d'autant plus que le climat peut causer de nombreux effets indirects, par exemple en modifiant les taux de perturbations de son habitat via un changement dans le régime des feux (Boulanger et al. 2013) ou en influençant l'accessibilité et l'abondance de la nourriture ainsi que le niveau de harcèlement causé par les insectes (Vors & Boyce 2009). Bien que

ces limitations n'invalident pas nos résultats, il y a de la place pour amélioration, en commençant par l'acquisition de données climatiques plus précises sur la couche et la structure de la couche nivale.

Réponse du caribou forestier aux perturbations naturelles et anthropiques

Malgré ces limitations, j'ai pu mettre en évidence que durant l'hiver le caribou forestier évitait, en moyenne, deux fois plus les aires de coupes forestières récentes que les aires de brulis récents dans l'ensemble de l'aire d'étude. Ce résultat était robuste à la présence d'autocorrélation spatiale dans les résidus des modèles. Pour faire cette comparaison, je me suis basé sur la perturbation d'origine et la hauteur des peuplements forestiers après perturbation (< 7 mètres) plutôt que sur l'âge des perturbations. Ce choix repose sur le fait que pour une même année depuis la dernière perturbation, la hauteur des peuplements après perturbation peut être très différente selon la productivité et l'historique des sites. De plus, il est probable que le caribou forestier réponde plus directement, de manière fonctionnelle, à la structure de la végétation (ex: couvert de fuite, stress environnemental, alimentation) plutôt qu'à l'âge de la perturbation *sensus stricto* ou encore à un indice de productivité des sites.

La réponse inégale du caribou forestier vis-à-vis des feux et des coupes invite à une réflexion dans le cadre de l'aménagement écosystémique, particulièrement en ce qui concerne les effets sur le caribou forestier d'une substitution des aires brulées par des aires de coupes de même intensité, de même superficie et ayant une répartition spatiale équivalente. Bien que le mécanisme sous-jacent à cette différence doive encore être identifié et quantifié avec précision, il est possible que l'évitement plus important des coupes soit directement lié à une densité élevée de chemins forestiers à l'intérieur ou à proximité de celles-ci. L'accroissement des densités de chemins diminuerait les coûts de déplacement des prédateurs (Houle et al. 2010), ce qui se traduirait par une recherche des proies plus efficace (DeCesare 2012) et donc un risque de prédation plus important dans les aires de coupes que dans les brulis récents. Cette hypothèse doit encore être vérifiée mais si tel est le cas, il sera nécessaire d'envisager des mesures correctrices, dans le cadre de l'aménagement écosystémique, qui incluent notamment une renaturalisation active des

réseaux de chemins forestiers par la végétation pour éviter leur utilisation prolongée par les prédateurs.

Les patrons de coupes présents dans cette étude vont jusqu'en 2005 c'est-à-dire peu de temps après la mise en œuvre des *objectifs de protection et de mise en valeur* (OPMV; *la Loi sur les Forêts, art. 35.6*) *5* et *6,* qui visent respectivement l'application de patrons de répartition spatiale des coupes adaptés à l'écologie régionale et la protection de l'habitat des espèces vulnérables ou menacées du milieu forestier. Ces patrons de coupes peuvent donc ne pas refléter les patrons ultérieurs tels que mis en oeuvre dans le cadre de la nouvelle stratégie sur l'aménagement durable des forêts (2010). Il sera donc important de mettre à jour la comparaison des effets des coupes *vs* des feux sur la distribution spatiale du caribou forestier en fonction de l'évolution des patrons de coupes à l'échelle des paysages. Par ailleurs, les inventaires répétés sur la présence/absence de réseaux de pistes à des échelles temporelles différentes permettront d'évaluer la dynamique temporelle dans la distribution du caribou forestier en fonction du type et de l'intensité des perturbations, ce qui ultimement fournira une information importante pour les gestionnaires.

Conservation du caribou forestier dans un contexte de régimes multiples de perturbation

Les stratégies actuelles de conservation du caribou forestier au Québec reposent en partie sur la protection de son habitat via la mise en place de zones de conservation à l'intérieur desquelles le développement des activités humaines est proscrit (Équipe de rétablissement du caribou forestier du Québec 2008, 2013). Peu d'études ont cependant évalué l'efficacité écologique d'une telle stratégie pour maintenir des populations stables ou en croissance en présence de régimes multiples de perturbation (e.g. coupes et feux) (voir Lesmerises et al. 2013). Réciproquement, la protection de paysages forestiers peut affecter le niveau et les coûts de récolte en matières ligneuses et donc influencer le développement socioéconomique de régions qui dépendent étroitement de l'exploitation des ressources ligneuses. Pour juger de l'efficacité des mesures de conservation dans un tel contexte, il est nécessaire de quantifier simultanément l'efficacité économique et écologique des mesures de conservation (Naidoo et al. 2006). J'ai donc développé dans ce dernier chapitre un

modèle dynamique de simulation spatialement explicite des paysages pour évaluer comment les zones de conservation pour le caribou forestier interagissaient dans le temps et l'espace avec les activités d'aménagement forestier et le régime des feux. Pour ce faire, je me suis inspiré de la stratégie de rétablissement du caribou forestier mise en place dans trois unités d'aménagement forestier (UAF) dans la région de la Côte-Nord au Québec.

Les principaux résultats montrent que lorsque les niveaux de récolte en volume de bois sont calculés sans prendre en compte de manière explicite les processus spatiaux que sont les feux et les blocs de protection pour le caribou forestier, les objectifs à moyen et long termes d'approvisionnement constant en volume de bois ainsi que les objectifs de conservation du caribou forestier ne sont rencontrés dans aucune des trois UAFs. L'absence de prise en compte des feux et des blocs de protection dans la détermination du niveau de possibilité forestière reflétait les hypothèses de calcul qui ont été utilisées jusqu'en 2013 pour déterminer annuellement le niveau de récolte en volume dans chaque UAF. Par ailleurs, la présence de coupes de récupération après feu n'a pas permis de diminuer les antagonismes entre l'atteinte des objectifs de conservation et d'aménagement forestier. En conséquence, si le but est de garantir un approvisionnement constant et à long terme en volume de bois tout en réunissant les conditions minimales pour maintenir des populations de caribou forestier stables ou en croissance, il apparait donc incontournable de réviser à la baisse les niveaux de récolte en matière ligneuse pour prendre en compte les contraintes imposées par le régime des feux et par l'ensemble des zones de conservation.

Limites des modèles dynamiques de simulation
Comme tout modèle, un modèle dynamique de simulation des paysages est une abstraction de la réalité et son élaboration est motivée avant tout par l'impossibilité pratique de manipuler de façon expérimentale et exhaustive les processus simulés. De plus, de nombreux processus demeurent peu prévisibles, ce qui contraint fortement les capacités prédictives d'un tel modèle. Par exemple, il est à ce jour très difficile de prédire la localisation et l'étendue exacte des feux qui auront lieu dans le futur. Un constat similaire peut être fait, sur un horizon de 150 ans, pour la localisation des blocs de coupe, des chemins ou encore des zones de conservation. Dans cette étude, l'utilité d'un tel exercice

est donc principalement de comparer des scénarios entre eux afin de quantifier l'importance des différents processus sur les indicateurs d'intérêt. Le fait d'avoir simulé de manière identique les feux, les patrons de coupes et la construction de chemins dans tous les scénarios permet de s'assurer que les comparaisons entre scénarios sont valides, même si les prédictions d'un scénario en particulier peuvent diverger de ce qui est réellement observé sur le terrain.

Parmi les limitations liées au présent modèle de simulation, je n'ai pas pu tenir compte de la nature temporaire et dynamique des blocs de protection comme indiquée dans le plan de rétablissement du caribou forestier 2005-2012 (Équipe de rétablissement du caribou forestier du Québec 2008). En effet la localisation à court, moyen et long termes des futurs massifs de remplacement n'était pas connue au commencement de cette étude. J'ai donc assumé que les blocs de protection actuels étaient permanents. Une meilleure connaissance de la localisation future des zones de conservation permettra de bonifier le présent modèle en dressant un portrait plus réaliste des modalités de conservation et des contraintes que ces modalités engendrent sur les activités d'aménagement forestier. À ce titre, les modalités de conservation telles que simulées (zones de conservation statiques) apparaissent probablement conservatrices en termes de contraintes pour l'aménagement forestier comparativement à des zones de conservation dynamiques.

Une autre limitation de mon modèle est d'avoir tenu compte exclusivement des effets de la perte d'habitat sur le taux de recrutement (nombre de faons/100 femelles), sans regard à la fragmentation des paysages et à la connectivité entre les parcelles d'habitat. Des résultats récents indiquent que des parcelles d'habitat faiblement connectées entre elles augmentent la vulnérabilité des caribous à la prédation par le loup gris (Courbin 2013). Au vu de ce résultat, il est donc vraisemblable que la relation entre le recrutement des faons et le taux de perturbation utilisée dans le sous-modèle de dynamique de population sous-estime l'effet réel de ces perturbations. En effet, le taux de perturbation tel que calculé par Environnement Canada (2012) ne tient pas compte directement de la connectivité entre les parcelles d'habitat, ni de leur agencement dans l'espace par rapport aux parcelles perturbées.

Conservation vs aménagement forestier: perspectives

L'efficacité d'une stratégie de conservation basée sur un réseau d'aires protégées se mesure tant au niveau écologique que socioéconomique (Naidoo et al. 2006). Au niveau écologique, il est crucial de continuer l'acquisition des connaissances sur les facteurs écologiques qui influencent la dynamique des populations de caribou forestier. La relation entre le taux de recrutement et le taux de perturbation, établie par Environnement Canada (2012), a l'avantage d'être simple mais elle mérite d'être bonifiée. Par exemple, on ignore à ce jour le temps nécessaire pour qu'une perturbation initiale redevienne un habitat utilisé par le caribou forestier, ce qui nécessite une part de subjectivité de la part des gestionnaires et des modélisateurs pour établir un seuil (ex : 40 ans dans cette étude). Par ailleurs, en plus du taux de perturbation, la fragmentation de la matrice forestière (Courbin 2013) et l'abondance de certains habitats situés à proximité des zones perturbées (Moreau et al. 2012) influencent les patrons de sélection d'habitats et donc pourraient également influencer la dynamique des hardes de caribou forestier. Une meilleure compréhension du rôle joué par ces facteurs augmenterait la précision des modèles de dynamique de population pour le caribou forestier.

Un modèle de simulation des paysages comme celui-ci bénéficierait aussi de l'inclusion d'un modèle centré sur l'individu (*individual based model*) capable de simuler plus finement les états biologiques et les mouvements des individus/hardes en fonction des changements dans la composition et la structure des paysages. La calibration de ce type de modèle n'est toutefois pas une entreprise triviale (Latombe 2013). De plus, réunir ce type de modèle avec des modèles de simulation des paysages dans un même exercice de simulation peut poser des défis majeurs en terme de temps de simulation.

Au niveau socioéconomique, on ne peut ignorer que la mise en place d'un réseau d'aires protégées permanent et/ou temporaire interagisse spatialement à l'échelle régionale avec le régime des feux et les activités d'aménagement forestier. Mon dernier chapitre montre que ces interactions ont un impact sur les niveaux d'approvisionnement en volume ainsi que sur les coûts de transports de bois. À ce titre, une baisse du niveau de récolte apparait incontournable par rapport aux hypothèses de calcul initiales si l'on souhaite garantir un

approvisionnement durable et constant en volume de bois dans les trois UAFs de la zone d'étude. La prochaine étape sera de quantifier l'amplitude de la baisse du niveau de récolte pour l'industrie forestière ainsi que d'évaluer le pourcentage de cette baisse qui est attribuable soit aux feux, soit aux zones de conservation pour le caribou forestier. Lorsque cette information sera disponible, elle fournira une meilleure idée du coût d'opportunité associé à la mise en œuvre du plan de rétablissement du caribou forestier dans cette région. Ce type d'information a le potentiel de réduire les conflits entre les différents protagonistes en favorisant l'adhérence des différents intervenants à une vision commune des enjeux et des solutions (Redpath et al. 2012)

Références

Beale, C. M., Lennon, J. J., Yearsley, J. M., Brewer, M. J. & Elston, D. A. (2010) Regression analysis of spatial data. *Ecology Letters* 13: 246-264.

Boulanger, Y., Gauthier, S., Gray, D. R., Le Goff, H., Lefort, P., & Morissette, J. (2013) Fire regime zonation under current and future climate over eastern Canada. *Ecological Applications* 23: 904-923.

Cabeza, M., Araújo, M. B., Wilson, R. J., Thomas, C. D., Cowley, M. J. R. & Moilanen, A. (2004) Combining probabilities of occurrence with spatial reserve design. *Journal of Applied Ecology* 41: 252-262.

Courbin, N. (2013) Intéractions entre le loup gris, le caribou forestier et l'orignal en forêt boréale aménagée. Thèse de doctorat. Université laval. 191p.

DeCesare NJ (2012) Separating spatial search and efficiency rates as components of predation risk. *Proceedings of the Royal Society B* 279: 4626-4633.

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.

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 + 138pp.

Équipe de rétablissement du caribou forestier du Québec (2008) Plan de rétablissement du caribou forestier (*Rangifer tarandus*) au Québec 2005-2012. Ministère des Ressources naturelles et de la Faune, Faune Québec, Direction de l'expertise sur la faune et des habitats, Canada.

Équipe de rétablissement du caribou forestier du Québec (2013) Lignes directrices pour l'aménagement de l'habitat du caribou forestier (*Rangifer tarandus caribou*), produit pour le compte du ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, 24 p. + 1 annexe.

Houle, M., Fortin, D., Dussault, C., Courtois, R. & Ouellet, J.-P. (2010) Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. *Landscape Ecology* 25: 419-433.

Illian, J. B., Martino, S., Sørbye, S. H., Gallego-Fernández, J. B., Zunzunegui, M., Esquivias, M. P. & Travis, J. M. (2013) Fitting complex ecological point process models with integrated nested Laplace approximation. Methods in Ecology and Evolution 4: 305-315.

Illian, J. B., Sorbye, S. H. & Rue, H. (2012) A toolbox for fitting complex spatial point process models using integrated nested Laplace approximation (INLA). *Annals of Applied Statistics 6: 1499-1530.*

Latombe, G. (2013) Développement d'un modèle centré sur l'individu des déplacements du caribou, du loup et de l'orignal, et de leurs interactions, en forêt boréale aménagée. Thèse de doctorat. Univerité de Montréal. 205 p. + annexes

Lesmerises, R., Ouellet, J.-P., Dussault, C. & St-Laurent, M.-H. (2013). The influence of landscape matrix on isolated patch use by wide-ranging animals: conservation lessons for woodland caribou. *Ecology and Evolution* 3: 2880-2891.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A. & Langtimm, C. A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83: 2248–2255.

Moreau, G., Fortin, D., Couturier, S., & Duchesne, T. (2012) Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. *Journal of Applied Ecology*, 49, 611-620.

Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006) Integrating economic costs into conservation planning. *Trends in Ecology & Evolution* 21: 681-687.

Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A. & Gutiérrez, R. J. (2012) Understanding and managing conservation conflicts. *Trends in Ecology & Evolution* 28: 100-109.

Renner, I. W., & Warton, D. I. (2013) Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics* 69: 274-281.

Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B-Statistical Methodology* 71: 319-392.

Sørbye, S. H., & Rue, H. (2013). Scaling intrinsic Gaussian Markov random field priors in spatial modelling. *Spatial Statistics*. In press.

Thuiller, W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* 9: 1353-1362.

Vors LS, Boyce MS (2009) Global declines of caribou and reindeer. *Global Change Biology* 15: 2626-2633.