Université du Québec à Rimouski

RESTAURER L'HABITAT DU CARIBOU PAR LE DÉMANTÈLEMENT DES CHEMINS FORESTIERS : RÉGÉNÉRATION VÉGÉTALE ET RÉPONSES DU CARIBOU, DE SES PRÉDATEURS ET DES PROIES ALTERNATIVES

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PAR

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RÉSUMÉ

Les populations humaines ne cessent de croître à travers le monde, résultant en l'augmentation des perturbations anthropiques qui sont reconnues pour menacer l'intégrité, la fonction et la biodiversité présente au sein des écosystèmes naturels. Parmi ces perturbations, les structures linéaires jouent un rôle important dans le déclin des populations boréales du caribou des bois (*Rangifer tarandus caribou*) en facilitant les déplacements des prédateurs et en augmentant les ressources alimentaires disponibles pour l'ours noir (*Ursus americanus*) et l'orignal (*Alces americanus*). La restauration de l'habitat du caribou par le biais du démantèlement des chemins forestiers s'avère donc susceptible de réduire les pressions de prédation sur le caribou. La présente étude visait à déterminer le type de démantèlement le plus efficace pour restaurer l'habitat du caribou boréal. Les quatre traitements étudiés suivaient un gradient d'intensité des efforts de restauration, soit des chemins : (1) fermés à la circulation humaine; (2) fermés et décompactés; (3) fermés, décompactés et plantés d'épinettes noires (*Picea mariana*); (4) fermés, décompactés, plantés et enrichis avec de la matière organique. Dans 101 sites d'échantillonnage répartis sur 40 km de chemins, nous avons évalué l'établissement de la végétation par le dénombrement des herbacées, arbustes et arbres. De plus, 232 caméras automatisées ont été installées afin d'évaluer l'utilisation des chemins par le caribou, le loup gris (*Canis lupus*), l'ours et l'orignal. L'établissement de la végétation sur les chemins ainsi que l'utilisation des chemins par le caribou étaient majoritairement influencés par les traitements de restauration. L'utilisation des chemins par les caribous, ours et les orignaux était influencée par l'utilisation par les autres espèces ainsi que par l'environnement adjacent. Nos résultats suggèrent que la combinaison de la fermeture, de la décompaction et de la plantation d'épinettes est le type de démantèlement le plus efficace pour restaurer l'habitat du caribou, car en plus d'augmenter le niveau d'utilisation des chemins par le caribou et de réduire la disponibilité alimentaire pour l'ours et l'orignal, ce traitement est plus susceptible de mener à terme à une pessière mature, l'habitat préférentiel du caribou. Nous suggérons que le démantèlement devrait être priorisé dans les secteurs comportant une forte proportion de milieux humides ou de coupes récentes afin de réduire l'efficacité de déplacement des prédateurs et proies alternatives qui utilisaient davantage les chemins adjacents à ces types de peuplement.

Mots clés : caméra automatisée, ours noir, préparation mécanique, *Rangifer tarandus caribou*, régénération de la végétation, restauration active, restauration de l'habitat, structures linéaires, système caribou-loup-orignal, utilisation des chemins forestiers

ABSTRACT

Human populations are continuously growing worldwide, increasing the prevalence of anthropogenic disturbances known to jeopardize the integrity, function and biodiversity of natural ecosystems. Linear features play an important role in the decline of boreal populations of woodland caribou (*Rangifer tarandus caribou*) by facilitating predator movements and increasing food resources for black bears (*Ursus americanus*) and moose (*Alces americanus*). The restoration of caribou habitat through the decommissioning of forest roads could thus reduce predation pressure exerted on caribou. This study aimed to identify the most effective road decommissioning treatment to restore boreal caribou habitat. The four treatments we studied followed an intensity gradient of restoration efforts, and consisted in: (1) closing the road to human traffic; (2) closing the road and decompacting its soil; (3) closing and decompacting the road, and planting black spruce trees (*Picea mariana*); (4) closing and decompacting the road, planting trees, and adding enriched soil (organic matter). In 101 sample sites distributed along 40 km of roads, we assessed vegetation establishment by counting herbaceous plants, shrubs, and trees. In addition, 232 motion-activated cameras were installed to assess road use by caribou, gray wolf (*Canis lupus*), black bear and moose. Restoration treatments explained vegetation establishment as well as road use by caribou. Road use by the caribou, bears, and moose was mainly influenced by the level of road use of other species as well as by the surrounding environment. Our results suggest that the combination of road closure, decompaction, and planting is the most effective type of decommissioning treatment to restore caribou habitat; in addition to increasing the level of road use by caribou and reducing food availability for bears and moose, this treatment was more likely to ultimately lead to mature spruce forests, the preferential habitat of caribou. We suggest that road decommissioning should be prioritized in areas with a high proportion of wetlands or recent clearcuts to reduce the movement efficiency of predators and alternate prey that used roads surrounded by these land covers more frequently.

Keywords: active restoration, black bear, camera-trap, caribou-wolf-moose system, forest road utilisation, habitat restoration, linear features, mechanical site preparation, *Rangifer tarandus caribou*, vegetation recovery

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INTRODUCTION GÉNÉRALE

La biodiversité mondiale est, aujourd'hui, principalement menacée par la perte, l'altération et la fragmentation des habitats naturels, la surexploitation des populations fauniques et floristiques (chasse, pêche, piégeage, cueillette et braconnage), la compétition directe ou indirecte induite par les espèces envahissantes, la pollution ainsi que les changements climatiques (Maxwell et al. 2016; WWF 2020). Toutes ces pressions sont associées à l'augmentation de l'activité humaine à l'échelle planétaire (WWF 2020). Au cours des dernières décennies, la superficie des zones agricoles, des pâturages, des plantations et des zones urbaines s'est largement étendue à l'échelle mondiale et ce, dans le but de répondre aux besoins grandissants des populations humaines (Foley et al. 2005). On distingue deux principaux types de perturbations anthropiques; en premier lieu, les perturbations dites « polygonales », qui comprennent entre autres les zones agricoles, les parterres de coupes forestières ou les sites miniers, mais aussi les perturbations linéaires, dont font partie les lignes sismiques, les routes et les chemins de fer (Pasher et al. 2013).

L'influence des perturbations anthropiques sur les espèces végétales et animales dépend de la capacité des espèces à s'adapter aux changements du milieu. En ce sens, les espèces sensibles aux changements de leur environnement (p. ex. espèces bioindicatrices; Aceto et al. 2003; Juma et al. 2018) répondent rapidement aux perturbations, alors que des espèces moins sensibles ou ayant une forte capacité d'acclimatation se verront moins affectées, voire favorisées. Par exemple, Danneyrolles et al. (2019) ont montré que les espèces d'arbres adaptées aux perturbations anthropiques ont été favorisées par les perturbations du 19e siècle dans l'est du Canada. Des observations similaires ont été notées dans le règne animal. Les animaux peuvent répondre aux perturbations anthropiques en modifiant leur comportement; lorsque ces changements comportementaux sont insuffisants, les perturbations anthropiques peuvent ultimement modifier la démographie des populations et la composition des communautés animales (Johnson & St-Laurent 2011). Par exemple, Ribeiro-Neto et al. (2016) ont montré que, dans les forêts tropicales brésiliennes, le niveau des perturbations influençait la structure des communautés de fourmis où certaines espèces profitaient des perturbations (p. ex. *Pheidole diligens*) alors que d'autres se voyaient défavorisées (p. ex. *Camponotus cingulatus*). Également, certains méso-carnivores, tels le coyote (*Canis latrans*), le raton-laveur (*Procyon lotor*) et le blaireau européen (*Meles meles*), bénéficieraient des ressources alimentaires et de la disponibilité en abris offertes dans les milieux urbanisés, ce qui augmenterait la densité de leur population (Bateman & Fleming 2012). À l'inverse, d'autres espèces sont menacées par les perturbations anthropiques. C'est le cas du sanglier à barbe (*Sus barbatus*), désigné vulnérable sur la Liste rouge des espèces menacées de l'Union Internationale pour la Conservation de la Nature, dont le déclin est lié à la perte et l'altération de son habitat (Luskin et al. 2017) causées par les activités humaines.

SITUATION DES POPULATIONS BORÉALES DU CARIBOU DES BOIS

Les populations boréales du caribou des bois (*Rangifer tarandus caribou*; ci-après caribou boréal) sont désignées menacées en vertu de la Loi sur les espèces en péril au Canada (LC 2002 c29) et vulnérables en vertu de la Loi sur les espèces menacées ou vulnérables au Québec (RLRQ c E-12.01 r2). Ces populations déclinent dans la presque totalité de l'aire de répartition de l'espèce au pays (COSEPAC 2014, 2016). Ce déclin serait principalement attribuable aux effets indirects des activités anthropiques modifiant l'habitat du caribou (Rettie & Messier 1998; Courtois et al. 2007; Vors et al. 2007; Johnson et al. 2015), particulièrement les perturbations affectant la relation avec ses prédateurs (Sorensen et al. 2008; Festa-Bianchet et al. 2011; Johnson et al. 2019). Par conséquent, la cause proximale du déclin serait la prédation exercée par le loup gris (*Canis lupus*) chez l'adulte (p. ex. Whittington et al. 2011; Mumma et al. 2018) ainsi que par l'ours noir (*Ursus americanus*) chez les faons, à tout le moins dans l'est du Canada (p. ex. Lambert et al. 2006; Dussault et al. 2012; Pinard et al. 2012). Afin d'atténuer les risques de prédation, les caribous utiliseraient une stratégie anti-prédatrice qui consisterait à s'isoler spatialement des prédateurs (Gustine et al. 2006; Pinard et al. 2012) et des proies alternatives, dont l'orignal (*Alces americanus*; Seip 1992; James et al. 2004). Ainsi, le caribou sélectionnerait les forêts matures d'épinettes noires (*Picea mariana*) et les tourbières (Courbin et al. 2009; Ray 2014) où le risque de prédation serait moindre (Courtois et al. 2002; Pinard et al. 2012).

L'aménagement forestier convertit les forêts de conifères matures en de jeunes peuplements feuillus propices aux cervidés (Cyr et al. 2009; Potvin et al. 2006; Bowman et al. 2010). Les zones en régénération qui sont générées par cet aménagement procurent une nourriture plus accessible, abondante, nutritive, énergétique et protéique (Rea et al. 2010; Denryter 2017). Cette disponibilité alimentaire favoriserait l'augmentation de l'abondance des populations d'orignaux, dont la productivité est plus élevée que le caribou (Potvin et al. 2005; Mumma et al. 2021). L'augmentation de la disponibilité des proies induirait, quant à elle, une réponse numérique du loup (Bowman et al. 2010; Festa-Bianchet et al. 2011). La présence croissante de ce prédateur dans l'aire de répartition du caribou augmenterait les probabilités de rencontres entre ces deux espèces, accentuant la prédation du loup sur le caribou (Seip 1992; Sorensen et al. 2008). Le caribou éviterait les zones perturbées à fine échelle (Vors et al. 2007; Leblond et al. 2011; Leclerc et al. 2012), mais ne serait pas suffisamment efficace à s'isoler de ses prédateurs et des proies alternatives afin de réduire les risques de prédation (Whittington et al. 2011). La configuration spatiale des forêts résiduelles au Québec (c.-à-d. l'association entre les coupes forestières et les forêts matures résiduelles) compliquerait l'évitement des zones perturbées et pousserait le caribou à utiliser davantage les coupes (Hins et al. 2009). De plus, la fragmentation du paysage réduirait la capacité des caribous femelles à déplacer leur domaine vital hivernal, les rendant prévisibles aux yeux des prédateurs, ce qui contribuerait à accroitre la pression de prédation (Lafontaine et al. 2017). À l'inverse, les caribous femelles seraient fidèles à leur domaine vital de mise bas, ce qui leur permettrait de mieux connaître la distribution des risques et des ressources, donc d'augmenter la probabilité de survie des faons (Faille et al. 2010; Lafontaine et al. 2017). Cependant, les perturbations anthropiques réduiraient la capacité d'exprimer cette fidélité (Courtois et al. 2007; Faille et al. 2010); le retour à un site récemment perturbé pourrait mener à un piège écologique (c.-à-d. la sélection d'un habitat risqué présentant les caractéristiques d'un habitat de qualité) en compromettant la survie des faons. La régénération végétale des sites perturbés augmenterait la disponibilité des ressources alimentaires pour l'ours (Dussault et al. 2012), ce qui risquerait d'accroitre leur abondance localement (Brodeur et al. 2008; Mosnier et al. 2008; Bastille-Rousseau et al. 2011). La stratégie anti-prédatrice utilisée par le caribou contre les loups s'avèrerait souvent inefficace et inadaptée contre les ours (Dussault et al. 2012; Pinard et al. 2012; Leblond et al. 2016). En effet, l'évitement des loups par les caribous durant la période où les jeunes sont vulnérables (Gustine et al. 2006) engendrerait une sélection des secteurs d'habitat également sélectionnés par l'ours (p. ex. coupes forestières de 6-10 ans; Leblond et al. 2016). De surcroît, les déplacements fréquents des ours entre leurs sites d'alimentation augmenteraient le taux de rencontres avec les couples mère–faon, résultant en une pression de prédation plus importante sur les faons (Bastille-Rousseau et al. 2011).

Outre la création de parterres de coupes, l'aménagement forestier comprend aussi la mise en place de routes forestières, des structures linéaires qui, en général, engendrent pour le caribou une perte fonctionnelle d'habitat, un risque accru de mortalité par collision et une limitation de l'accès à la nourriture et aux partenaires reproducteurs en raison de l'évitement exprimé par les individus face aux structures linéaires (Polfus et al. 2011). Le caribou est reconnu pour éviter les structures linéaires actives (c.-à-d. utilisées et entretenues) davantage que celles abandonnées et ce, à plusieurs échelles spatiotemporelles (Leclerc et al. 2012; Mumma et al. 2018, 2019). Leblond et al. (2011) ont montré qu'une forte densité de structures linéaires réduisait la disponibilité de l'habitat fonctionnel en périphérie, ce qui diminuait globalement la qualité de l'habitat du caribou. Plus cette densité est élevée, plus la capacité d'éviter les structures linéaires serait contrainte (Leblond et al. 2011), les taux de recrutement et de croissance démographique seraient bas (Whittington et al. 2011) et les risques de mortalité seraient élevés (Leblond et al. 2013; Rudolph et al. 2017; Mumma et al. 2018). À l'inverse, il a été montré que les orignaux seraient attirés près des structures linéaires par la végétation disponible, abondante (même hâtivement au printemps) et très nutritive (Rea et al. 2010; Laurian et al. 2012; van Rensen et al. 2015). Cependant, les orignaux éviteraient les secteurs présentant un volume de circulation automobile élevé (Laurian et al.

2008; Beyer et al. 2013). L'augmentation de l'abondance de l'orignal près des routes est de plus susceptible d'attirer son principal prédateur, le loup (Bowman et al. 2010; Courbin et al. 2014), qui sélectionnerait les structures linéaires pour se déplacer plus rapidement et efficacement (Finnegan et al. 2018a; Dickie et al. 2017a, b, 2020). Il a d'ailleurs été montré que la distance parcourue quotidiennement ainsi que le taux de recherche (c.-à-d. la combinaison de la distance parcourue, la zone de détection d'une proie et la proportion des rencontres menant à une capture) étaient plus élevés sur les structures linéaires qu'en forêt (Dickie et al. 2017a). Tigner et al. (2014) ont montré que les ours utilisaient également les structures linéaires pour se déplacer. Ces derniers pouvaient y retrouver des ressources alimentaires abondantes au printemps (p. ex. graminées; Mosnier et al. 2008; Bastille-Rousseau et al. 2011) et à l'automne (p. ex. arbustes fruitiers; Switalski & Nelson 2011). Les déplacements plus efficaces sur les structures linéaires permettraient aux prédateurs de mieux parcourir leur territoire et donc augmenter la probabilité de rencontre avec le caribou (Festa-Bianchet et al. 2011; Whittington et al. 2011; Mumma et al. 2018, 2019).

Sans mesures de gestion active, le déclin des caribous persiste et s'accentue (Hervieux et al. 2013; Wittmer et al. 2013). Par exemple, le contrôle des loups en Alberta a contribué à ralentir le déclin du caribou (Hervieux et al. 2013). Toutefois, l'arrêt du contrôle mènerait à l'augmentation rapide de l'abondance des prédateurs, l'approche ne s'avérant donc efficace qu'à court terme (Wittmer et al. 2013). Le contrôle des proies alternatives (réduction indirecte des prédateurs) favoriserait, quant à lui, la survie des caribous adultes, sans toutefois accroitre le recrutement (Serrouya et al. 2017). Bien que l'état des populations du caribou nécessite la mise en place urgente d'approches efficaces à court terme afin de diminuer le facteur proximal du déclin des populations (c.-à-d. la prédation), il est primordial de réduire le facteur ultime de ce déclin, soit la perturbation de leur habitat (Festa-Bianchet et al. 2011). Ainsi, il est important de simultanément mettre en place des stratégies de conservation efficaces à moyen et long termes, telles que la protection et la restauration de l'habitat (Vors & Boyce 2009; Ray 2014). Il a été suggéré que les perturbations totales (c.-à-d. les zones brûlées ainsi que les perturbations anthropiques linéaires et polygonales) ne devraient pas excéder 35 % de la superficie de l'aire de répartition d'une population locale de caribou afin d'offrir une probabilité d'autosuffisance de 60 % (c.-à-d. une population stable ou croissante; Environnement Canada 2012). La restauration de l'habitat pourrait permettre de réduire le niveau des perturbations à un niveau soutenable pour les populations de caribou (Ray 2014).

RESTAURATION DE L'HABITAT

La littérature scientifique dans le domaine de la restauration des écosystèmes, portant entre autres sur l'évaluation de l'efficacité des différentes approches de restauration, est plutôt récente (Wortley et al. 2013), soulignant le besoin d'accroître notre compréhension des facteurs influençant l'efficacité des mesures mises en place (Suding 2011). Bien que le but ultime de la restauration soit d'augmenter la probabilité de persistance des écosystèmes naturels et de rétablir leurs fonctions, son succès dépend des objectifs (le remplacement, la reconstruction, la réclamation et la réhabilitation) motivant les interventions (Stanturf et al. 2014). Tout d'abord, le remplacement a pour but d'imiter la migration d'une espèce qui serait engendrée par les changements climatiques, lorsque celle-ci est limitée par les barrières anthropiques (Stanturf et al. 2014). Par exemple, Castellanos-Acuña et al. (2015) ont planté des semences de populations de pins mexicains (*Pinus devoniana*, *P. leiophylla* et *P. pseudostrobus*) à de plus hautes altitudes que les populations souches dans le but de rétablir les populations en fonction des projections de données climatiques futures. À plus fine échelle, la reconstruction vise le retour à la communauté végétale d'origine avant l'utilisation des terres pour d'autres ressources (Stanturf et al. 2014). Par exemple, la plantation de 24 espèces d'arbres indigènes dans les pâturages avait pour but de restaurer les forêts tropicales en Australie (Charles et al. 2018). Lorsque la restauration est appliquée dans des paysages fortement altérés par les perturbations anthropiques, particulièrement par l'extraction de ressources souterraines telles que les mines (p. ex. Dhar et al. 2020), il s'agit plutôt de réclamation (Stanturf et al. 2014). Finalement, la réhabilitation consiste à restaurer la composition des espèces, la structure ou les processus écologiques d'un écosystème perturbé (Stanturf et al. 2014). Malgré que le but ultime de ce type de restauration soit le retour à l'état climax (c.-à-d. à l'écosystème naturel représentatif du climat; *sensu* Clements 1916, 1936), la restauration fonctionnelle est souvent utilisée pour les espèces menacées ou en voie de disparition (Stanturf et al. 2014) telles que les populations du caribou boréal (p. ex. Keim et al. 2019).

Puisque les perturbations linéaires facilitent les déplacements du loup et de l'ours (Tigner et al. 2014; Dickie et al. 2017a), et augmentent les ressources alimentaires pour l'ours et l'orignal (Bastille-Rousseau et al. 2011; Laurian et al. 2012), leur démantèlement s'avère une approche potentiellement efficace pour réduire les déplacements et la disponibilité alimentaire des proies alternatives et prédateurs du caribou. Le démantèlement des chemins forestiers est susceptible de permettre la réhabilitation des conditions optimales favorables au retour d'une forêt mature, conduisant au rétablissement de l'habitat essentiel des caribous (Finnegan et al. 2018b, 2019; Filicetti et al. 2019). La restauration de l'habitat par l'entremise du démantèlement des structures linéaires peut être réalisée selon plusieurs méthodes visant à limiter la vitesse de déplacement des prédateurs et proies alternatives qui sont favorisés par ces structures ou à faciliter l'établissement de la végétation (p. ex. Filicetti et al. 2019; Keim et al. 2019). Il a été suggéré que la végétation présente dans les structures linéaires limitait la vitesse de déplacement des prédateurs (Tigner et al. 2014; Dickie et al. 2017b). En ce sens, certains projets de restauration de l'habitat du caribou boréal ont testé l'ajout d'obstacles dans les structures linéaires dans le but d'entraver le mouvement des prédateurs. Par exemple, Keim et al. (2019) ont ajouté des troncs d'arbres aux intersections de lignes sismiques en Alberta. Cette étude a effectivement montré que l'ajout d'obstacles réduisait le déplacement des humains, des prédateurs et des proies alternatives. Cependant, ce type de restauration, bien qu'efficace à court terme, ne vise pas la restauration de l'habitat du caribou, à savoir le retour à un peuplement forestier résineux mature.

Plusieurs projets de restauration se sont intéressés à la reprise végétale dans les structures linéaires, de manière passive ou active (Figure 0.1). La restauration passive consiste à laisser les structures linéaires se régénérer naturellement. Cependant, l'abandon des structures linéaires permet tout de même le passage de véhicules qui maintiennent la compaction du sol (Lee & Boutin 2006), limitant la croissance d'essences ligneuses et ultimement le recouvrement végétal (Sutherland 2005; Lee & Boutin 2006). En effet, St-

Pierre et al. (2021) ont montré que 22 % des chemins forestiers en restauration passive n'avaient aucune régénération végétale. Il a également été montré que 35 ans après la fin des activités d'extraction pétrolière dans l'Ouest canadien, seulement 8,2 % des lignes sismiques étaient recouvertes à plus de 50 % d'espèces ligneuses, alors que 65 % des lignes revégétalisées conservaient une végétation herbacée (Lee & Boutin 2006). Il a été montré que la fermeture seule des chemins forestiers (c.-à-d. sans passage de véhicules) ne permettait pas un retour à un habitat forestier, puisque 35 ans après la fermeture de chemins en Gaspésie, 22 % des chemins présentaient toujours une assise intacte (SÉPAQ 2014). De plus, il a été noté que la circulation automobile réduisait l'utilisation des structures linéaires par les loups (Hebblewhite & Merrill 2008; Lesmerises et al. 2012; Dickie et al. 2017a) et les orignaux (Laurian et al. 2008; Beyer et al. 2013). Ces derniers pourraient donc être favorisés par l'absence de dérangement sur des chemins fermés à la circulation automobile. Le fort rayonnement solaire observé sur les structures linéaires dû à l'absence d'un couvert végétal favoriserait la reprise d'espèces végétales recherchées par l'ours (Mosnier et al. 2008; Switalski & Nelson 2011) et l'orignal (Rea 2003; Rea et al. 2010; Laurian et al. 2012). La régénération peut donc différer considérablement de l'habitat présent avant les perturbations (Zang & Ding 2009; Finnegan et al. 2018b) et mener vers un peuplement feuillu au lieu d'un peuplement résineux, par exemple (St-Pierre et al. 2021). Ainsi, la restauration active qui implique la mise en place d'interventions permettant de démanteler les structures linéaires, comme par exemple le grattage ou la décompaction du sol et la plantation de semences ou d'arbres (Kolka & Smidt 2004; Switalski & Nelson 2011; Tarvainen & Tolvanen 2016; Dickie et al. 2021), semble nécessaire afin de réduire le chevauchement spatial entre le caribou et ses prédateurs (Finnegan et al. 2018b).

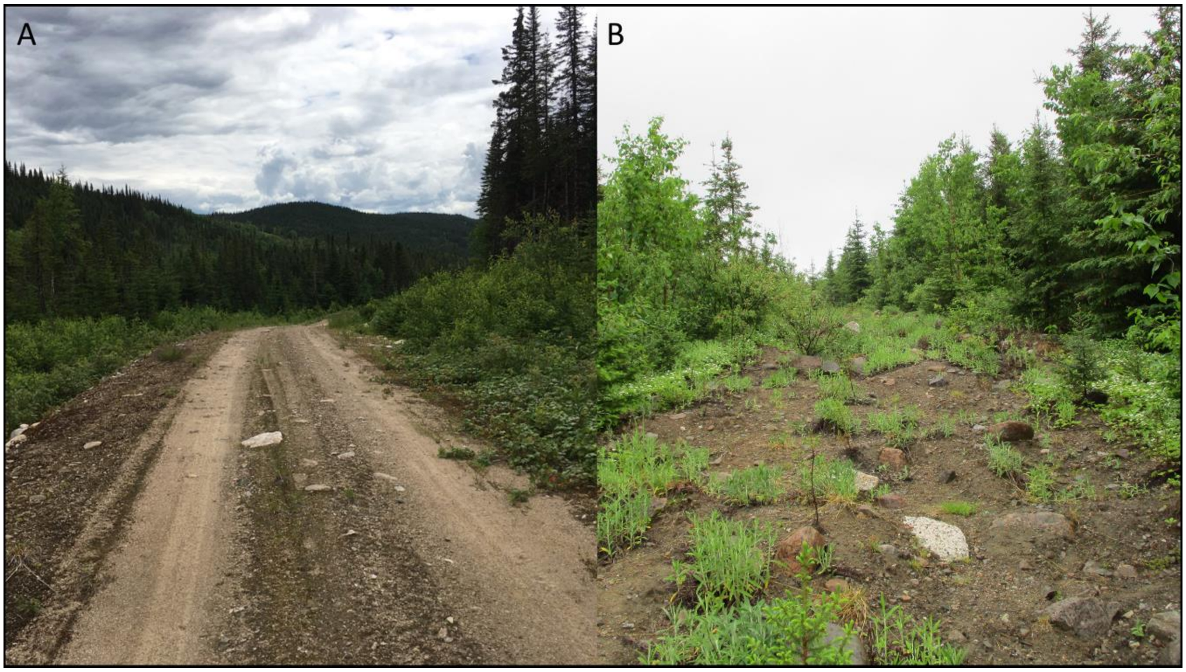

Figure 0.1 : Illustration de l'état de la végétation recolonisant passivement l'assise d'un chemin forestier de 10 ans (A; crédit photo : Fabien St-Pierre) par rapport à un chemin forestier de 4 ans ayant fait l'objet d'efforts de restauration active (B; crédit photo : Rebecca Lacerte)

Au Canada, la majorité des travaux de restauration a été réalisée dans l'ouest du pays et portait sur le démantèlement des lignes sismiques (p. ex. Filicetti et al. 2019; Dickie et al. 2021). Peu d'efforts ont été investis pour étudier les retombées de la restauration active des chemins forestiers, qui pourtant s'avèrent fonctionnellement et structurellement très différents des lignes sismiques (Figure 0.2). En effet, les lignes sismiques sont principalement associées à des paysages perturbés par l'exploration pétrolière et gazière. Ces exploitations s'effectuent sur le court terme seulement, et ne nécessitent donc pas de structures durables. Par conséquent, la création des lignes sismiques permet l'utilisation d'une machinerie réduisant les impacts sur la végétation et la surface du sol (Government of the Northwest Territories 2015). À l'inverse, les chemins forestiers sont créés afin de supporter l'exploitation forestière de manière récurrente et à plus long terme, entre autres pour le transport du bois, ce qui nécessite une préparation de terrain impliquant l'utilisation d'une machinerie lourde. En effet, la création de ces chemins nécessite l'ajout de matière inorganique (gravier, agrégats, sable) afin de stabiliser et compacter la surface de roulement (Desautels et al. 2009). En outre, les lignes sismiques sont plus étroites que les chemins forestiers; alors que les lignes sismiques modernes peuvent être aussi étroites que 2 m (elles étaient plus larges avant les années 1990; voir Dabros et al. 2018), les chemins forestiers font généralement jusqu'à 15-20 m de largeur (Desautels et al. 2009). Il a été montré que l'établissement de la végétation et l'utilisation des structures linéaires par les mammifères variait en fonction des caractéristiques des structures linéaires (p. ex. la largeur, la longueur ou la sinuosité) et de l'environnement entourant les structures linéaires (van Rensen et al. 2015; Filicetti et al. 2019; Dickie et al. 2017a). Considérant les différences fonctionnelles et structurelles entre les lignes sismiques et les chemins forestiers, il est probable que l'établissement de la végétation et l'utilisation des chemins forestiers par les mammifères diffère de ce qui a été observé sur les lignes sismiques. Ainsi, il est nécessaire de s'intéresser au démantèlement des chemins forestiers afin d'évaluer l'efficacité de la restauration de l'habitat du caribou boréal.

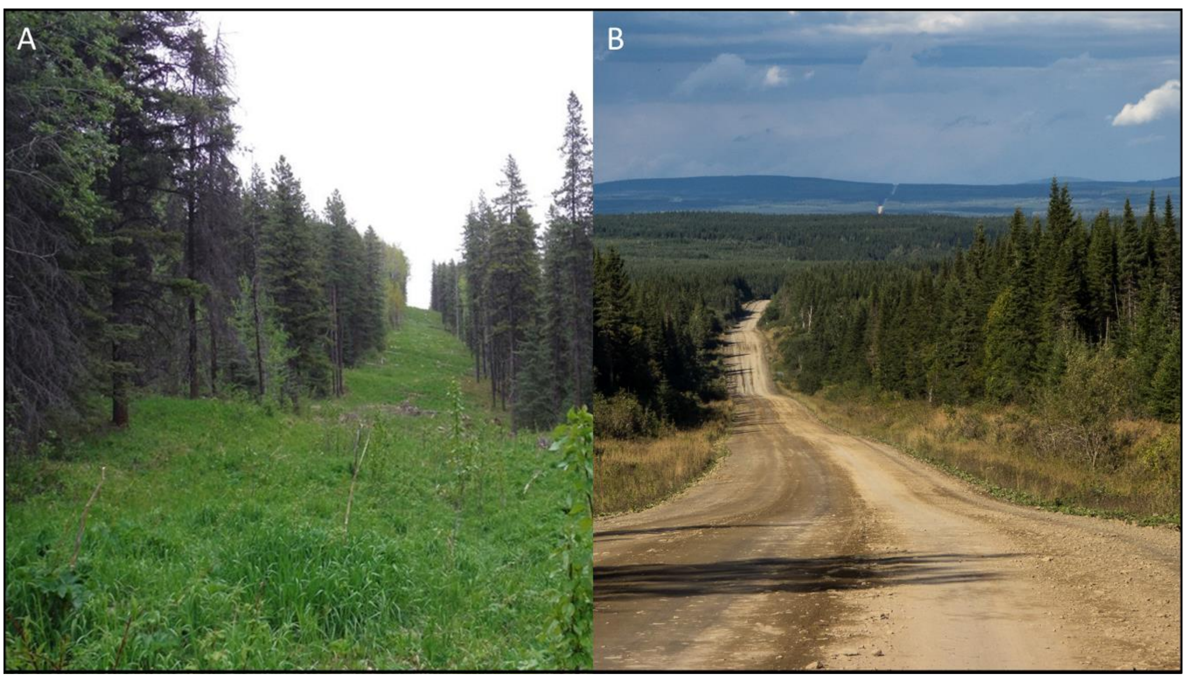

Figure 0.2 : Illustration d'une ligne sismique (A; crédit photo : fRI Research) et d'un chemin forestier (B; crédit photo : E. Huybrechts)

OBJECTIFS, HYPOTHÈSES ET SURVOL DES PRINCIPAUX RÉSULTATS

L'objectif principal de ce mémoire était d'évaluer l'effet à court terme de quatre traitements de démantèlement de chemins forestiers sur l'établissement de la végétation ainsi que sur leur utilisation par une communauté de grands mammifères, dans le but d'évaluer l'efficacité de ces traitements à restaurer l'habitat du caribou boréal. Les traitements suivaient un gradient d'intensité de restauration, où chaque traitement comprenait le traitement précédent : (1) chemin fermé à la circulation humaine; (2) chemin fermé et décompacté; (3) chemin fermé, décompacté et planté avec des plants d'épinette noire; (4) chemin fermé, décompacté, planté et enrichi avec de la matière organique. En outre, des chemins actifs ont servi de témoins dans les analyses sur l'établissement de la végétation. Les traitements ont été réalisés par le Conseil de la Première Nation des Innus Essipit afin de générer un habitat favorable au caribou boréal à l'échelle de leur Nitassinan et ce, dans le but ultime d'augmenter la connectivité fonctionnelle entre les populations de Lac-des-Cœurs (notre aire d'étude) et de Pipmuacan, située plus au nord. Mon premier objectif était d'évaluer l'effet des quatre traitements de restauration active sur l'établissement de la végétation, incluant les herbacées, les arbustes et les arbres, 3 à 4 ans après les travaux de restauration. Mon second objectif consistait à décrire l'influence des traitements sur l'utilisation des chemins forestiers démantelés par le caribou boréal, le loup gris, l'ours noir et l'orignal, 1 à 3 ans après les travaux de restauration.

En lien avec mon premier objectif (chapitre 1), j'ai émis l'hypothèse que l'établissement de la végétation dans les chemins forestiers serait influencé par l'intensité des efforts de restauration (traitements), mais également par l'environnement adjacent aux chemins. Pour le deuxième objectif (chapitre 2), j'ai énoncé l'hypothèse que la disponibilité des ressources (c.-à-d. la végétation pour les herbivores, les proies pour les carnivores et ces deux ressources pour les omnivores) sur les chemins forestiers (ou à proximité), ainsi que le risque de prédation pour les proies, influenceraient l'utilisation des chemins forestiers démantelés par les caribous, les loups, les ours et les orignaux. Dans le but de vérifier l'hypothèse du chapitre 1, j'ai utilisé des données de végétation récoltées dans 101 sites répartis dans les quatre traitements ainsi que sur les chemins témoins. Dans chacun des sites, j'ai dénombré l'ensemble des tiges de toutes les espèces végétales sur une surface de 40 m^2, en plus de mesurer les caractéristiques structurelles des segments de chemin. Pour le second chapitre, j'ai utilisé les photos de 322 caméra-années (n = 161 caméras) à détection automatique dispersées dans les quatre traitements pour générer une probabilité et une intensité d'utilisation des chemins par le caribou, le loup, l'orignal et l'ours. J'ai également utilisé 141 caméra-années (n = 71 caméras) distribuées dans l'environnement adjacent aux chemins de manière à prendre en compte les variations de densité locale de ces grands mammifères. Pour les deux chapitres, j'ai caractérisé l'environnement adjacent au dispositif d'échantillonnage dans des zones tampons de 250 m à 1 km à l'aide d'un système d'informations géographiques.

Les résultats du premier chapitre illustrent que l'établissement de la végétation dans les chemins forestiers était expliqué à 25 % par les types de traitement. La largeur du chemin ainsi que la composition de l'environnement adjacent aux chemins influençaient également la distribution de la végétation dans les chemins. Le traitement fermé, décompacté et planté, en plus de réduire la disponibilité de l'abondance des ressources alimentaires pour l'ours et l'orignal (c.-à-d. la présence et l'abondance d'herbacées, d'arbustes fruitiers et d'arbres feuillus), diminuait aussi la présence d'espèces susceptibles d'entrer en compétition avec l'épinette noire (p. ex. éricacées). Les résultats du second chapitre révèlent que seulement les caribous étaient directement influencés par les traitements de restauration; pour cette espèce, le traitement planté était davantage utilisé que le traitement fermé. Malheureusement, nous n'avons pas pu tester l'utilisation des chemins par les loups, car trop peu de loups ont été capturés par les caméras. Néanmoins, l'utilisation des chemins par les caribous, les ours et les orignaux était principalement influencée par l'utilisation des chemins faite par les autres espèces ainsi que par l'environnement adjacent aux chemins forestiers. Les caribous utilisaient davantage les segments de chemin retrouvés dans des secteurs supportant une densité locale élevée d'ours, mais faible d'orignal. Les ours utilisaient les segments utilisés par les caribous, alors que les orignaux utilisaient davantage les chemins utilisés par les loups. De plus, les caribous utilisaient davantage les routes adjacentes à une forte proportion de forêts résineuses, et les ours utilisaient les routes avoisinant des milieux humides. Finalement, les orignaux étaient plus présents sur les routes adjacentes à des perturbations naturelles ou des coupes forestières récentes. Les résultats principaux de mon mémoire suggèrent que le traitement de démantèlement des chemins forestiers le plus efficace pour restaurer l'habitat du caribou boréal combine la fermeture du chemin à la circulation automobile, la décompaction du sol ainsi que la plantation d'épinettes noires. Ce traitement, en plus d'augmenter l'utilisation des chemins par le caribou, est susceptible de mener à une pessière mature, l'habitat préférentiel du caribou boréal (Courbin et al. 2009; Ray 2014).

CHAPITRE 1
DÉTERMINANTS DE LA RÉGÉNÉRATION DE LA VÉGÉTATION SUR LES CHEMINS FORESTIERS APRÈS TRAITEMENTS DE RESTAURATION : IMPLICATIONS POUR LA CONSERVATION DU CARIBOU BORÉAL

1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Le démantèlement des structures linéaires a été identifié comme solution à long terme pour restaurer les habitats perturbés par le développement anthropique. Peu d'études se sont intéressées à l'efficacité du démantèlement des chemins forestiers, qui est pourtant la perturbation linéaire la plus importante dans l'est du Canada. De telles connaissances permettraient d'améliorer les efforts de conservation des populations boréales du caribou des bois (*Rangifer tarandus caribou*). En effet, les chemins forestiers augmentent la disponibilité alimentaire pour l'ours (*Ursus americanus*) et l'orignal (*Alces americanus*; et donc pour le loup *Canis lupus*, principal prédateur de l'orignal) et facilitent les déplacements des prédateurs, ce qui accroit la prédation sur le caribou. Nous avons donc évalué l'établissement de la végétation dans quatre traitements de restauration répartis sur 40 km de chemins forestiers, le long d'un gradient de traitements additifs (c.-à-d., chaque traitement successif incluait le traitement précédent): fermeture de la route à la circulation, décompaction du sol, plantation d'épinettes noires (*Picea mariana*) et ajout de terre enrichie. Le couvert latéral ainsi que l'abondance et l'occurrence des espèces végétales sur les chemins démantelés ont été mis en relation avec les traitements de restauration et les variables environnementales. L'établissement de la végétation 3 ou 4 ans après les travaux de restauration a principalement été influencé par le type de traitement, mais également par la composition des peuplements à proximité des chemins. Sur le plan de la régénération végétale, le traitement le plus efficace était celui qui combinait la fermeture, la décompaction et la plantation, car il diminuait la

présence d'espèces compétitrices à l'épinette ainsi que la disponibilité alimentaire pour l'ours et l'orignal. Le succès à court terme de ce traitement suggère qu'une telle pratique pourrait profiter au caribou en établissant une régénération qui devrait conduire à des peuplements forestiers résineux matures favorables au caribou et défavorables à ses prédateurs.

J'ai rédigé ce premier article, intitulé « *Determinants of vegetation regeneration on forest roads following restoration treatments: Implications for boreal caribou conservation* », en collaboration avec mon directeur Martin-Hugues St-Laurent, professeur en écologie animale à l'Université du Québec à Rimouski, et mon codirecteur Mathieu Leblond, chercheur scientifique à Environnement et Changement climatique Canada. Cet article a été publié dans sa version finale en septembre 2021 dans *Restoration Ecology* (volume 29, numéro 7, e13414; https://doi.org/10.1111/rec.13414), une revue scientifique internationale à comité de révision par les pairs. En tant que première auteure, ma contribution comprenait la récolte et la gestion des données sur le terrain, l'essentiel des analyses statistiques et géomatiques, ainsi que l'écriture et la révision du manuscrit. Mes co-auteurs ont supervisé l'étude et coordonné le financement, en plus d'également participer à l'écriture et à la révision de l'article. Une version abrégée de cet article a été présentée au congrès de la Société Québécoise pour l'Étude Biologique du Comportement (SQÉBC) en novembre 2020 et 2021, à l'Équipe de rétablissement du caribou forestier au Québec en mars 2021, au *18th North American Caribou Workshop* (NACW) en mai 2021, au 14e colloque annuel du Centre d'Étude de la Forêt (CEF) en mai 2021 ainsi qu'au *9th World Conference on Ecological Restoration* (SER) en juin 2021.

1.2 DETERMINANTS OF VEGETATION REGENERATION ON FOREST ROADS FOLLOWING RESTORATION TREATMENTS: IMPLICATIONS FOR BOREAL CARIBOU CONSERVATION

ABSTRACT

Linear features are increasing worldwide and, in many jurisdictions, their decommissioning has been identified as a way to restore wildlife habitat. Few studies have assessed restoration practices on forest roads, yet they are the main linear disturbance throughout most circumboreal forests. In boreal forests of eastern Canada, such knowledge would be especially valuable for the conservation of boreal populations of woodland caribou (*Rangifer tarandus caribou*). We assessed the short-term establishment of vegetation following four treatments applied across 40 km of forest roads, along a restoration gradient involving additive treatments (i.e., each successive treatment included the treatments prior): closing the road to traffic, decompacting the soil, planting black spruce (*Picea mariana*) trees, and adding enriched soil. We linked lateral cover (a proxy of movement obstruction for wildlife) and the occurrence and abundance of plant species to road treatments and environmental covariates. Vegetation establishment 3 to 4 years after decommissioning was mostly influenced by treatments but also by road width and stand composition in the vicinity of roads. The combination of closing, decompacting, and planting was the most effective treatment to establish regeneration that would lead to suitable caribou habitat as it reduced food availability for moose (*Alces americanus*) and bears (*Ursus americanus*; i.e., lower presence of herbaceous species, fruit-bearing shrubs, and deciduous trees). It also reduced the presence of plants competing with spruce, such as ericaceous shrubs. Our results suggest that the decommissioning of forest roads could benefit caribou, provided it is performed at a sufficiently broad scale, and accompanied by other habitat restoration and protection practices.

INTRODUCTION

Anthropogenic disturbances are ubiquitous in Canada's boreal ecosystems, where they are estimated to affect 24 million ha (Pasher et al. 2013). These disturbances have the potential to influence wildlife and plants through impacts on individuals, populations and, ultimately, whole food webs and ecosystem dynamics (Johnson & St-Laurent 2011). Linear disturbances such as roads can alter the physical and chemical environment, propagate exotic species, increase animal mortality, and limit their access to food and mates (Trombulak & Frissell 2000). Considering their pervasiveness and broad consequences over entire ecosystems, it is imperative that abandoned linear features be restored to the extent feasible in order to preserve natural environments.

Throughout the world, surveys conducted on abandoned linear features have shown that they often supported no vegetation (Lee & Boutin 2006; St-Pierre et al. 2021), or that natural regeneration did not result in vegetation communities that are representative of their pre-disturbance state (Zang & Ding 2009; Finnegan et al. 2018a). Restoration projects relying on the decommissioning of roads have shown that vegetation regeneration could be influenced by treatments such as closing, ripping, recontouring, and planting of tree seeds (Kolka & Smidt 2004; Switalski & Nelson 2011; Tarvainen & Tolvanen 2016). In Canada's boreal forests, the response of vegetation on seismic lines (through both passive and active restoration) has been shown to vary according to line characteristics and surrounding environment (van Rensen et al. 2015; Filicetti et al. 2019; Finnegan et al. 2019), but very few studies have assessed vegetation recovery on forest roads (but see St-Pierre et al. 2021). This is a significant knowledge gap because seismic lines, mostly found in western Canada, differ from forest roads of eastern Canada in both structure and function (Pasher et al. 2013). Forest roads are created to facilitate the transport of wood and are thus built with the addition of material (often sand) to stabilise the surface and support heavy machinery over a long period of time. Because of this, soil compaction is usually important on roads (Desautels et al. 2009). In contrast, modern machines used to clear low-impact seismic lines nowadays are designed to reduce damage to the vegetation and ground surface (Government of the Northwest

Territories 2015). Seismic lines may be as narrow as 2 m (Dabros et al. 2018), whereas logging roads are at least 15–30 m wide (Desautels et al. 2009). Because of these differences between seismic lines and forest roads, and considering the variability observed among linear features in the response of vegetation to restoration treatments, results found in past studies may be expected to differ for forests roads in eastern Canada. It is especially relevant to assess vegetation regrowth after active restoration because techniques such as road decommissioning are expected to be increasingly used by land managers for the conservation of threatened species.

Linear features have been shown to have a significant role in the decline of boreal populations of woodland caribou (*Rangifer tarandus caribou*; hereafter boreal caribou; e.g. Rudolph et al. 2017; Mumma et al. 2018), a species designated as threatened under the Species at Risk Act in Canada. Similar observations have been made for reindeer (*R.t. tarandus*) in Scandinavia (Skarin & Åhman 2014). Boreal caribou are associated with old-growth black spruce forests and boreal peatlands, where they can find the plants and lichens that compose their diet while spatially segregating from their predators and alternate prey (Courbin et al. 2009; Ray 2014). Linear features increase the probability that caribou die from predation (Leblond et al. 2013; Mumma et al. 2018) by facilitating the movements of their predators (e.g. Finnegan et al. 2018b; Dickie et al. 2020), and by providing food resources to black bears (*Ursus americanus*; Bastille-Rousseau et al. 2011) and alternate prey such as moose (*Alces americanus*; Laurian et al. 2012). Environment Canada (2011) suggested that anthropogenic disturbances (including linear features) should occupy less than 35% of a boreal caribou range to offer a 60% probability of maintaining a stable or increasing caribou population. Active restoration of linear features could re-establish natural regeneration conditions and help restore parts of boreal caribou ranges that are heavily disturbed by roads (Finnegan et al. 2018a, 2019; Filicetti et al. 2019).

In this study, we examined the short-term effectiveness of four treatments to restore boreal caribou habitat by improving the regeneration of vegetation on forest roads. Our treatments were, in increasing order of intensity, (1) closing roads, (2) closing and decompacting the soil to favor natural regeneration, (3) closing, decompacting, and planting black spruce (*Picea mariana*) trees, and (4) doing all of the above and adding enriched soil (see *Methods* for details). We tested the last treatment to assess whether enriched soil would favor the growth of planted black spruce trees (i.e., by providing essential nutrients) or, alternatively, would favor other competing plants. We also monitored untreated roads as controls. Our treatments aimed at establishing vegetation regeneration that would eventually lead to mature black spruce stands favorable to boreal caribou, but we measured the occurrence and abundance of all plants present on road segments, including all trees, shrubs and herbaceous plants. We hypothesized that the establishment of vegetation on forest roads would be influenced by treatment type, as well as by the environment surrounding road segments. We predicted that the number of black spruce stems and lateral cover would increase with treatment intensity. We also predicted that the colonization of treated road segments by natural regeneration would be representative of the availability of plant species in the nearby forest, with the more abundant species having a higher probability of colonizing treated roads.

METHODS

Study area

The study area was located in the projected biodiversity reserve Akumunan (70°08′ W, 48°44′ N) managed by the Essipit First Nation and located northeast of the Saguenay River in Québec, Canada (Fig. 1.1). The 285-km^2 area is located in the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain, with a subarctic humid continental climate (Robitaille & Saucier 1998). The mean temperature for the growing season (May-September) was 14.7°C and the mean precipitation was 88.4 mm (Environment Canada 2020). The study area was located close to the meridional limit of the continuous distribution of boreal caribou in Québec.

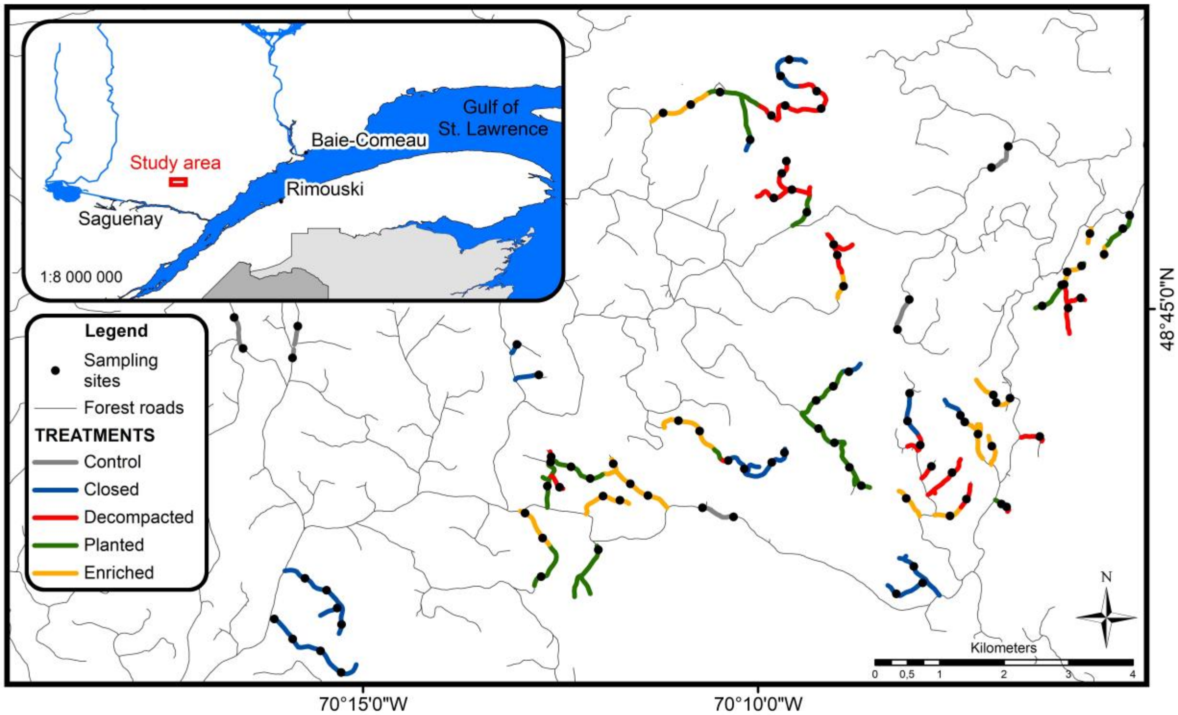

Figure 1.1: Study area in the projected biodiversity reserve Akumunan (70°08′ W, 48°44′ N), located northeast of the Saguenay River in Québec, Canada. Forty kilometers of roads were decommissioned to restore boreal caribou habitat

Road restoration treatments

To study vegetation establishment after the decommissioning of forest roads, we evaluated four treatments distributed across 40 km of forest roads in our study area. Road age prior to treatments was estimated to be no older than 20 years. Each treatment was randomly assigned to road segments (1 km or less in length), for a total of 10 km of treated roads per treatment (or slightly less due to logistical constraints). Additionally, 5 km of non-closed roads were used as controls. The Essipit First Nation coordinated restoration activities in 2015 and 2016. For the first treatment, road segments were closed to human circulation by placing large boulders, digging trenches, placing the removed material at the entrance of road sections to create an obstacle, and adding a sign indicating that the road was closed (hereafter the "closed road" treatment; Fig. 1.2a). In the second treatment, road segments were closed and their soil was decompacted using an excavator (hereafter the "decompacted" treatment;

Fig. 1.2b). Soil decompacting was performed at a depth of 30 to 40 cm, and coniferous trees already present due to natural regeneration were preserved as much as possible. In the third treatment, road segments were closed, decompacted, and planted with black spruce stems (hereafter the “planted” treatment; Fig. 1.2c). Planted stems were 30 cm in height on average, and were obtained from a nursery. In the fourth treatment, road segments were closed, decompacted, planted, and organic matter (garden soil) was added at the base of each planted tree to stimulate growth (hereafter the “enriched” treatment; Fig. 1.2d). A total of 30,000 trees (or 1,500 per linear km) were planted in the planted and enriched treatments during the summer of 2016.

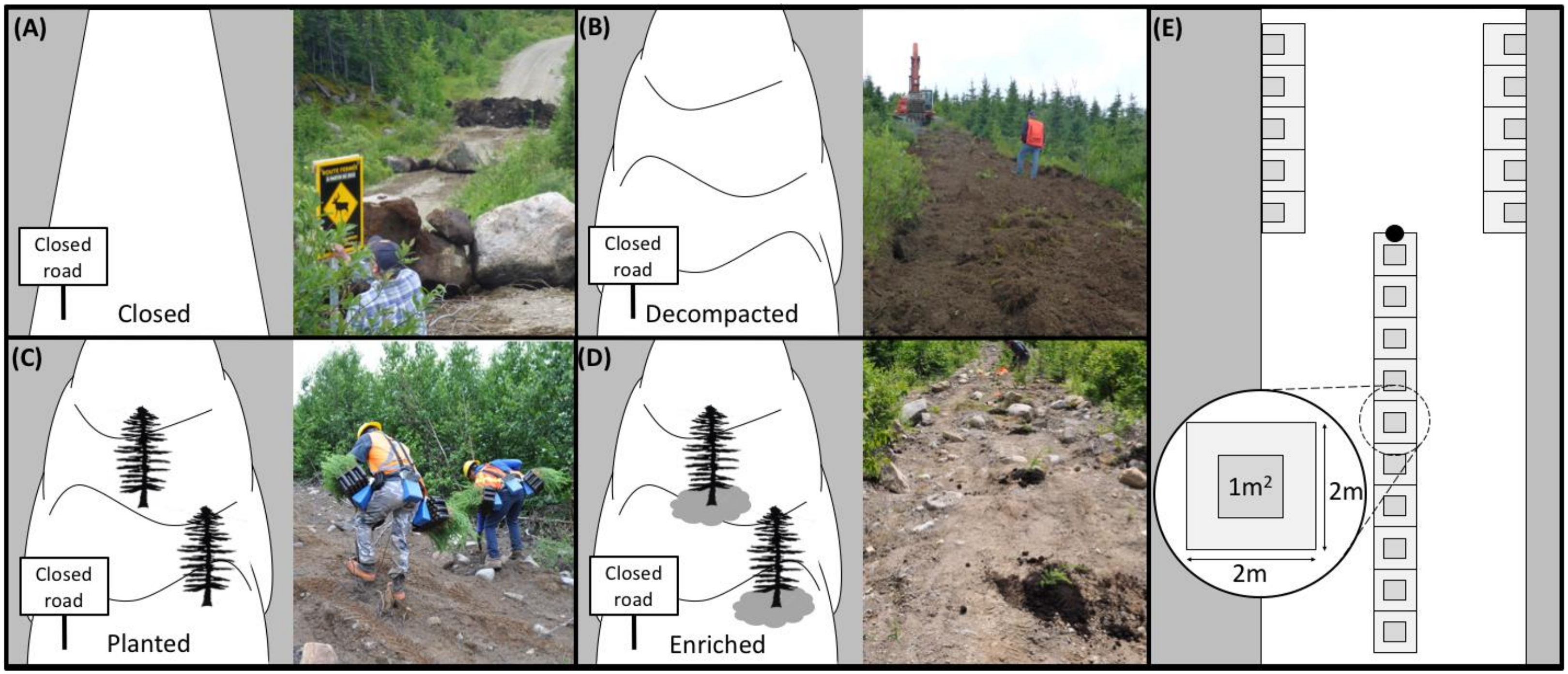

Figure 1.2: Schematization of the four road treatments, i.e., closed road (A), decompacted (B), planted (C), and enriched treatments (D; see text for details), and the 20 4-m^2 and 1-m^2 plots composing each sampling site (E). Lateral cover and other road characteristics were determined in the center of the road (black dot on panel E).

Plant regeneration

We characterized vegetation regeneration (including planted trees) in the four treatments and in the non-treated controls 3 or 4 years after restoration work. We randomly distributed sampling sites (30 m in length) on road segments, separated by a minimal distance of 400 m, for a total of 101 sites (i.e., 10 controls, 23 closed roads, 22 decompacted, 23 planted, and 23 enriched). Each sampling site was composed of 20 plots of 4-m^2, i.e., 10 in the center of the road, 5 on the right side, and 5 on the left (Fig. 1.2e). We assessed vegetation regeneration by counting the number of stems for each tree and shrub species in all 4-m^2 plots. Additionally, we evaluated the establishment of herbaceous plants, including forbs and graminoids, by counting their stems (or tussocks for graminoids and hawkweed *Hieracium* spp.) on 1-m^2 plots placed in 4-m^2 plots (see Fig. 1.2e). We tried to identify each stem at the species level, but we were sometimes forced to group them by genus or functional group (e.g. graminoids) when identification was not possible in the field. It was often impossible to differentiate planted from natural black spruce, so we counted all spruce stems without distinction. At the center of each site, we also estimated the percentage of lateral cover following the methods of Nudds (1977), by using a profile board with four height classes at 50-cm increments from the ground, to inform on the level at which plants obstructed animal movement.

Environmental context

We evaluated the influence of various environmental variables on vegetation regeneration (Table 1.1). We first measured road width and determined orientation, latitude and longitude at each sampling site. We estimated land cover type on a geographic information system in ArcGIS v.10.3 (ESRI 2018), using reclassified digital vegetation maps (1:20,000) provided by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP). These maps had a minimum mapping unit size of 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies), and were updated every year to account for natural and anthropogenic disturbances. We generated seven land cover categories (see Table 1.1) by calculating the percentage occupied by each category within a 250-m radius buffer centered on each sampling site. We created a Digital Elevation Model (DEM) using a Triangulated Irregular Network generated from hypsometric curves available in the Québec Topographic Database (1:20,000) to extrapolate elevation at each sampling site. Finally, we created a slope raster from the DEM to estimate slope at each site.

Table 1.1: Description of the environmental variables determined at sampling sites.

Environmental variables	**Description**
Road width (m)	Measured using a measuring tape
Road orientation (°)	Determined using a compass
Latitude, Longitude	Determined using a handheld GPS
Elevation (m)	Extrapolated from the Digital Elevation Model (DEM)
Slope (°)	Estimated from the slope raster obtained from the DEM
Land cover (%)	Seven land cover categories in a 250-m radius buffer surrounding sampling sites: 1) deciduous, 2) mixed-wood, 3) coniferous forests, 4) wetlands, 5) natural disturbances (fires, windthrows and insect epidemics), 6) recent clearcuts (≤20 years old), and 7) old clearcuts (>20 years old)

Statistical analyses

Effects of environmental variables and treatment types on the abundance of species

We performed a partial canonical correspondence analysis (pCCA; ter Braak & Verdonschot 1995; Kenkel 2006) to characterize the associations between plant species among sampling sites, while simultaneously considering their response to environmental variables and to road treatments. In this analysis, we used the number of stems of each species as response variables (Appendix 1.1), and we used treatments (four treatments and controls) and environmental variables as predictor variables. We summed all stems or tussocks belonging to the same sampling site (i.e., all stems from the 20 4-m^2 plots) and used sampling sites as the sampling unit. To use a similar sampling surface across species (4-m^2), we multiplied by four the number of herbaceous plants and graminoids counted in 1-m^2 plots. The pCCA is sensitive to species that are abundant in a few sites, but rare or absent in most sites (Kenkel 2006), thus we performed a Hellinger transformation on the number of stems to avoid giving too much weight to rare species (Legendre & Gallagher 2001). However, as reported by Legendre & Gallagher (2001), this transformation does not always eliminate the disproportionate weight of rare species, which, in our case, continued to generate convergence problems. Therefore, we ran our pCCA only on species observed in at least 20% of sites (Appendix 1.1). In the final pCCA (computed on species observed in at least 20% of sites), we combined all herbaceous species (namely hawkweed, fireweed [*Chamerion angustifolium*], pearly everlasting [*Anaphalis margaritacea*] and dwarf dogwood [*Cornus canadensis*]) and graminoids into one group (hereafter herbaceous species). We also included elevation, latitude and longitude as covariates to consider their influence on the summer growth of plants (Pausas & Austin 2001). We used the Variance Inflation Factor (VIF) to diagnose multicollinearity between environmental variables and covariates, and aimed to keep all covariates below a VIF of 5 (Oksanen et al. 2019). We removed recent clearcuts from our analyses because they generated high multicollinearity. We tested the significance of the model, axes, and predictor variables using a permutation test in the *vegan* package in R (Oksanen et al. 2019; R Core Team 2019).

Effects of treatment types on the occurrence of species

We were interested in assessing the specific effects of treatments on the availability of plant species for caribou, their predators and alternate prey. That could not easily be determined using a multivariate analysis, thus we ran generalized linear mixed models for each species separately using species occurrence instead of stem abundance. We did so because stem abundance was often null at the sampling plot level, resulting in non-normality (as determined using a Shapiro-Wilk Normality Test; Shapiro & Wilk 1965) and non-homogeneity of residuals (as determined using a Bartlett Test of Homogeneity of Variances;

Bartlett 1937) as well as high overdispersion (as determined using the *DHARMa* package; Hartig 2020). We thus coded all sites where a given species had a positive stem count as 1 (presence) and all sites where the species was absent as 0 (absence), and documented the variation in the occurrence of species across treatments using a mixed logistic regression model. We included forest road ID and sampling week as random effects to control for spatial autocorrelation and the growth of plants throughout summer. We conducted these analyses using the lme4 package (*glmer* function; Bates et al. 2015) in R. We compared the estimated means of treatments using post hoc EMM tests (*emmeans* package; Lenth et al. 2021). We verified the deviations from the expected distribution (Kolmogorov–Smirnov distribution test and outlier test), compared the standardized residuals and predicted values (quantile regression; *DHARMa* package; Hartig 2020), and tested the difference with the null model (likelihood ratio test). Assumptions were respected for herbaceous species, creeping snowberry (*Gaultheria hispidula*), blueberry (*Vaccinium* spp.), willow (*Salix* spp.), white birch, trembling aspen (*Populus tremuloides*), balsam fir and black spruce models, but not for raspberry (*Rubus* spp.) and currant (*Ribes* spp.) models, even when combined, likely because of a skewed distribution of absences across treatment types. Therefore, for the occurrence of raspberry and currant, we only present summary statistics (Appendix 1.2).

Effects of treatment types on lateral cover

To highlight the influence of treatment types on lateral cover, we used a zero-inflated beta mixed regression, a model adapted for values ranging between 0 and 1 (Ferrari & Cribari-Neto 2004). To do so, we converted cover percentage (0–100) into proportions (0–1). We only kept lateral cover from the ground up to 1 m, because only 15 sites (14.9%) had vegetation greater than 1 m in height. Given that beta regressions do not allow values of exactly 1 (in the *glmmTMB* package; Brooks et al. 2020), we changed the few values of 1 to 0.999 as suggested by Damgaard & Irvine (2019). Again, we included forest road ID and sampling week as random factors. We tested the deviations from the expected distribution of our model, the comparison of standardized residuals against the predicted values (quantile regression; *DHARMa* package; Hartig 2020), the beta distribution (of data and residuals), and the divergence between random effects. The statistical test assumptions were respected.

RESULTS

Abundance of plants on treated roads

The pCCA linking the variation in the number of plant stems to treatment types and environmental variables was significant (*P*=0.01; Appendix 1.3). The first three axes respectively explained 25.2, 5.1, and 2.9% of the variation across sampling sites, but the second and third axes were respectively marginally significant (*P*=0.10) and not significant (*P*=0.77), respectively. The first axis (*P*=0.01) contrasted treatment types, with closed roads farthest to the left, and decompacted, planted, enriched treatments, and control roads distributed along this axis from left to right (CCA 1: Fig. 1.3). Treatments (*P*=0.01), old clearcuts (*P*=0.04) and road width (*P*=0.01) influenced the number of stems in sampling sites, whereas deciduous stands (*P*=0.08) and slope (*P*=0.10) were marginally significant (Appendix 1.4). The 95% confidence ellipses of the four treatments differed from controls. The ellipses of the three most intensive treatments (i.e., decompacted, planted, and enriched) overlapped and were distinct from closed roads (Fig. 1.3). Black spruce stems were more abundant in closed road treatments. There were more trembling aspen, willows, blueberries, and creeping snowberries in closed roads, as well as in roads close to old clearcuts. The abundance of balsam fir and white birch stems was positively influenced by road width. Herbaceous species, raspberries, and currants were more abundant in the three most intensive treatments.

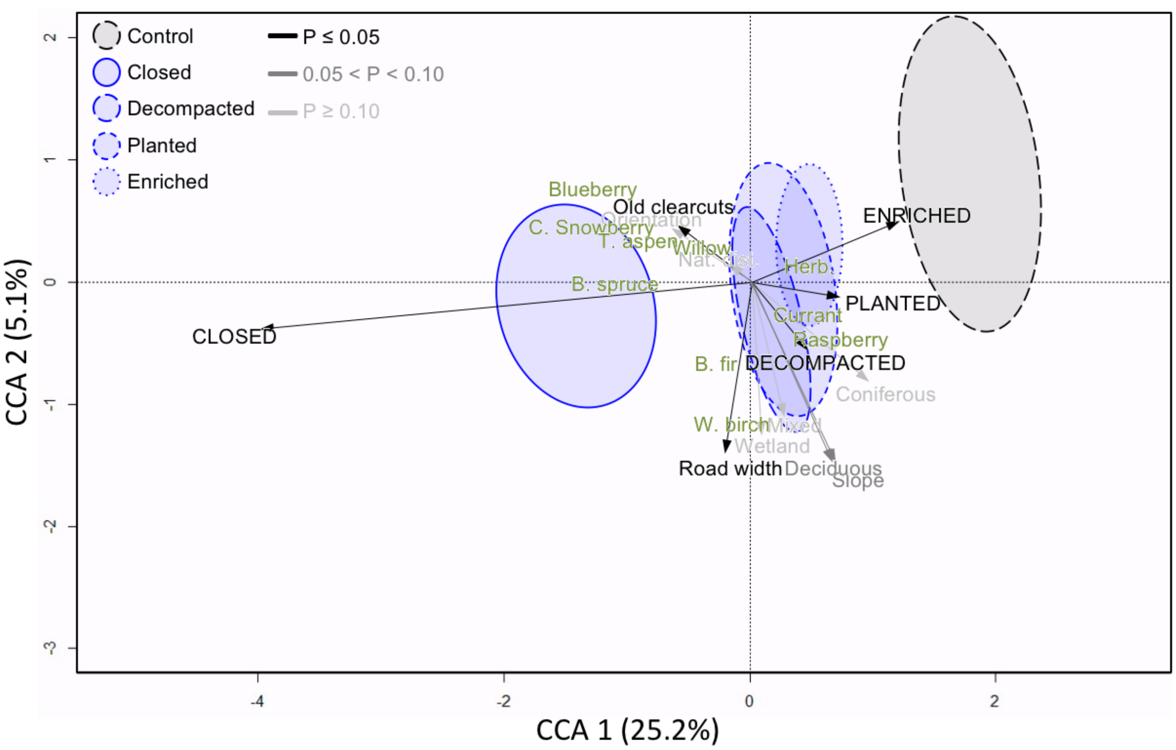

Figure 1.3: First two axes of the partial canonical correspondence analysis (pCCA) linking the number of stems of plant species (or species groups) present in more than 20% of sampling sites to treatments, and environmental variables used to assess vegetation regeneration in treated roads. Ellipses represent 95% confidence intervals of each treatment

Occurrence of plants relative to treatments

The fit of all species-specific logistic regression models describing the effects of treatments on vegetation occurrence was high (area under the Receiver Operating Characteristic curve ≥0.77). Models showed a lower probability of occurrence in controls compared to treatments for most species (i.e., black spruce, balsam fir, white birch, willow, and herbaceous species; Fig. 1.4), except for the less common species in our study area (i.e., creeping snowberry, blueberry, and trembling aspen). The occurrence of the latter in controls was much more variable (Fig. 1.4). We found a lower probability of occurrence of white birch stems in both planted and enriched sites compared to closed roads. The probability of occurrence of herbaceous plants was higher on both decompacted and enriched roads compared to closed roads. Interestingly, the probability of occurrence of black spruce stems (including planted trees) was lower in decompacted sites than in any other treatment, and was higher in closed and planted sites.

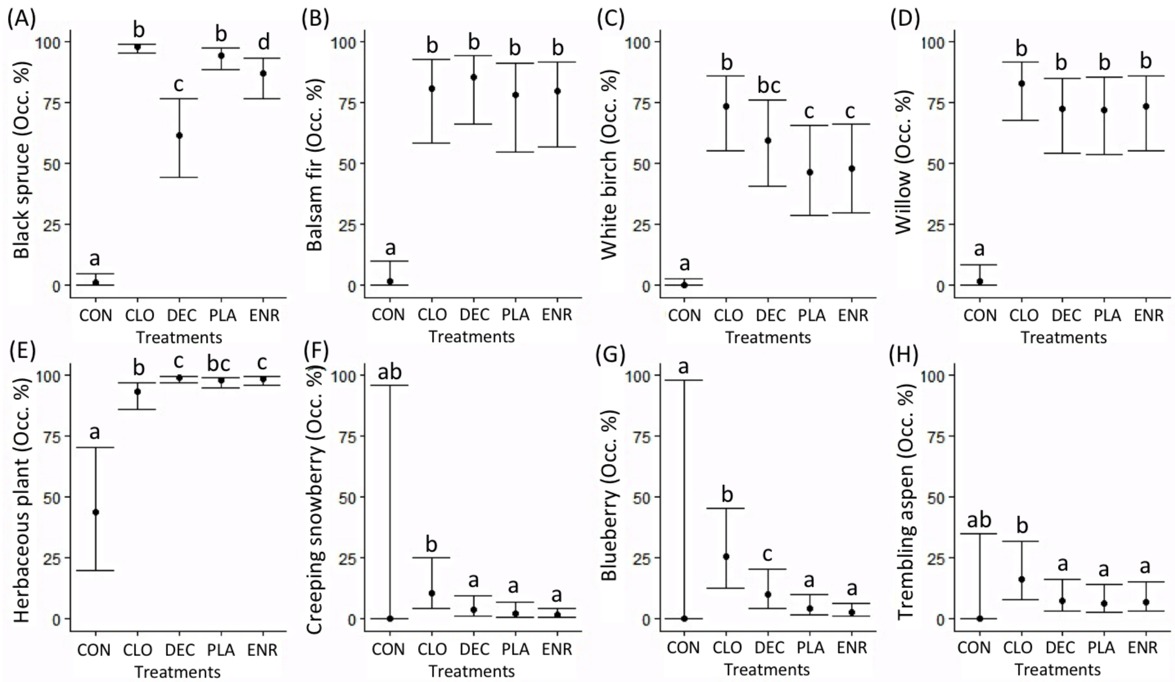

Figure 1.4: Probability of occurrence (Occ.%, with error bars showing 95% CI of the predicted values) of at least one stem in a 4-m^2 plot of black spruce (A), balsam fir (B), white birch (C), willow (D), herbaceous plants (E) creeping snowberry (F), blueberry (G), and trembling aspen (H) according to control roads (CON) and treatments (closed [CLO], decompacted [DEC], planted [PLA] and enriched [ENR]), determined using mixed logistic regression models. Lowercase letters show significant differences ($P \leq 0.05$) as determined using post hoc EMM tests.

Lateral cover

The binomial step of the zero-inflated beta regression analysis showed a lower probability of occurrence of lateral cover 1 m above ground in controls versus treated roads ($P<0.01$), but no significant difference between treatments (Fig. 1.5a). The conditional part of the model did not highlight any difference between treatments ($P \geq 0.19$; Fig. 1.5b).

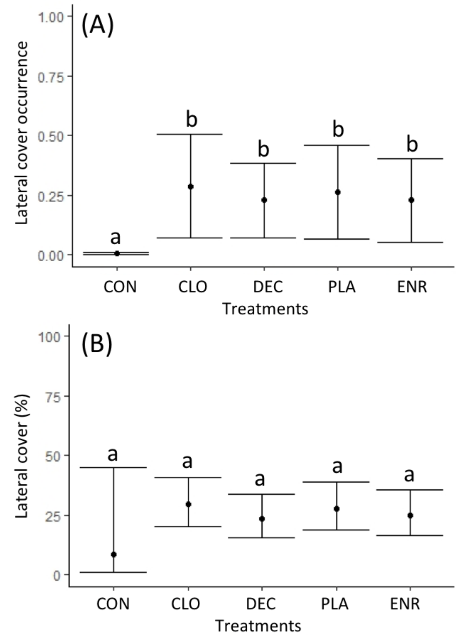

Figure 1.5: Probability of occurrence (with error bars showing 95% CI of the predicted values; A) and percentage (with error bars showing 95% CI; B) of lateral cover from ground level to 1 m according to control roads (CON) and treatments (closed [CLO], decompacted [DEC], planted [PLA] and enriched [ENR]) determined using a zero-inflated beta mixed regression. Lowercase letters show significant differences ($P \leq 0.05$) as determined using post hoc EMM tests

Discussion

Linear features such as forest roads and seismic lines have been shown to favour alternate prey and predators of caribou by increasing food availability and facilitating the movements of gray wolves (*Canis lupus;* Dickie et al. 2020) and bears (Tigner et al. 2014). Together, these effects can increase predation pressure on caribou (e.g., Leblond et al. 2013; Mumma et al. 2018). Few studies have evaluated the regeneration of vegetation on decommissioned forest roads, and how this approach could restore the quality and function of caribou habitat (Ray 2014). One such study in which researchers closed forest roads in the Gaspésie National Park (Québec, Canada) found that natural regeneration re-established in less than 22% of forest roads 35 years after they were closed (passive restoration; SÉPAQ

2014). In our study, we aimed to evaluate the effectiveness of several treatments to restore boreal caribou habitat on decommissioned forest roads in the boreal forest of eastern Canada. Treatments were the predictor variable that best explained species establishment across our study area, but we also found that the intensity of management interventions could benefit some plant species while hampering others. Similarly, several other studies worldwide have shown that plant abundance often differed among restoration treatments (Switalski & Nelson 2011; Tarvainen & Tolvanen 2016; Filicetti et al. 2019), suggesting that appropriate planning and long-term monitoring may be needed to meet expected restoration goals.

Control roads continued to be used by vehicles in our study area, which likely increased soil compaction and could have damaged or killed freshly regenerated stems, thus limiting vegetation abundance, composition, and lateral cover, as observed by St-Pierre et al. (2021). We could not determine the degree of human use in our study area, but the abundant regeneration in some sites (including control roads) suggests that at least some roads had been abandoned before the beginning of our study. This could explain the high variability we observed between control site replicates, as expressed by their large 95% confidence ellipses in the pCCA. This explanation also applies to closed sites, which were only closed to vehicles and not modified in any other way, and which also showed high inter-site variability.

We recognize that other variables not considered in our study could have explained the establishment of plant species on forest roads, as evidenced by the 71% unexplained variance in our pCCA analysis. For instance, we did not measure the seed bank in the soil, which can influence the establishment of species (Pinno & Hawkes 2015; Hart & Chen 2008). However, Grant et al. (2011) found that the active seeding of decommissioned roads did not influence native species cover. Moreover, we could not control for the effects of seed dispersal over broad areas (but see *Effects of the environment surrounding forest roads* below), which, for some species, can span multiple kilometers (e.g., *Betula* spp.; Kremer et al. 2012). Finally, we did not measure soil conditions, which can influence the establishment of species through impacts on soil nutrients, wetness, or temperature (Tremblay et al. 2013; Finnegan et al. 2019).

Effects of road decommissioning treatments

Plant regeneration in our sampling design was largely influenced by natural succession and the life history traits of colonizing plant species. Herbaceous species, which generally colonize disturbed areas first (Hart & Chen 2008), were more present in recently disturbed treatments (mainly decompacted and enriched roads). Other, more dominant species of shrubs and trees, such as blueberries and deciduous trees, likely outcompeted herbaceous species for access to light and reduced their occurrence and abundance in planted and closed sites (Pinno & Hawkes 2015; Dhar et al. 2020b; Reicis et al. 2020). The higher abundance of black spruce in closed treatments suggests that time since disturbance may be an important factor to explain vegetation regeneration on decommissioned roads. Indeed, vegetation was not removed by soil decompaction on closed roads, as opposed to other treatments, which allowed spruce, a species representative of late succession stages (Paquette et al. 2016), to grow. We note that naturally regenerated black spruce stems in closed roads were generally very small. We did not systematically measure plant height in this study, which prevented us from making conclusions concerning the biomass of plant species in our design.

The occurrence of black spruce stems was highest on planted sites, and lowest in decompacted sites, suggesting that decompacting, when done alone, did not benefit the natural establishment of black spruce, substantiating their late succession nature (Paquette et al. 2016). Thus, the plantation allowed for a higher occurrence of black spruce, compared to the newly-implemented natural regeneration observed in decompacted treatments. Furthermore, Tremblay et al. (2013) observed that mechanical site preparation could increase the survival of plantations. We showed that adding organic matter (garden soil) did not increase the establishment of black spruce, but slightly increased the occurrence of herbaceous species. Herbaceous species seemed better suited for acquiring the additional nutrients contained in the added soil. Although Man & Lieffers (1999) have mentioned potential advantages of a dense plant cover for spruce growth by providing favorable temperature and humidity conditions, our results suggest that competition likely had a stronger negative effect on spruce growth than the added benefits that these other plants could have provided. Adding soil with narrower C:N ratios, higher soluble potassium, and available phosphorus (Mackenzie & Naeth 2010) could increase species richness, diversity, and the cover of regenerating plants, especially for herbaceous species (Dhar et al. 2020a). This strategy may not be ideal for boreal caribou habitat restoration, however, because these highly palatable herbaceous species could attract more alternate prey (Rea et al. 2010; Laurian et al. 2012), as well as their predators (Bastille-Rousseau et al. 2011; Switalski & Nelson 2011). Herbaceous species also do not provide the barrier-effect to predator movements that larger trees and shrubs may have. In contrast, planted spruce trees could, in the long term, reduce encounter rates between caribou and its predators by hampering predator movements (McKenzie et al. 2012; Tigner et al. 2014; Dickie et al. 2020).

The response of blueberries to mechanical site preparation has been shown to vary across studies (Pinno & Hawkes 2015; Henneb et al. 2019; Dhar et al. 2020a, 2020b). It is important to consider ericaceous shrubs in the monitoring of caribou habitat restoration because their presence can decrease mineralizable NH_4^+-N in the soil and increase phenolic concentrations (Bloom & Mallik 2006; Reicis et al. 2020), which reduce black spruce growth through nutrient competition and allelopathic effects (Henneb et al. 2019; Ménard et al. 2019). In our study, blueberries were rare in the three decompacted treatments, especially in planted and enriched sites, suggesting that they were inhibited by soil decompaction and planting. Other ericaceous shrubs like sheep laurel (*Kalmia angustifolia*) and Labrador tea (*Rhododendron groenlandicum*) were rare at the scale of our study area, but abundant at a few sites, which could hinder black spruce establishment (Bloom & Mallik 2006; Reicis et al. 2020).

The lower presence of white birch and trembling aspen stems in the three most intensive treatments suggests that treatments involving decompacting and especially planting limited the establishment of deciduous trees. Deciduous trees usually outcompete black spruce in the first years following soil disturbance (Légaré et al. 2004; Ménard et al. 2019), but raspberries, currants and herbaceous species, which seemed to benefit from soil decompacting in our study, could have limited birch and aspen growth through light competition by covering the entire surface of the road (Archambault et al. 1998).

Effects of the environment surrounding roads

Stand composition in the vicinity of forest roads contributed to explaining the abundance of plant species on sampling sites. This is not surprising, considering that most plant species in our study area are dispersed by seeds, and that canopy composition strongly influences understory communities (Fourrier et al. 2015). In our study, adjacent old clearcuts (>20 years old) favored the establishment of trembling aspen, willows and blueberries, especially on closed roads. Trembling aspen and blueberries are commonly found in logged areas (Reicis et al. 2020), and are known to compete with black spruce (Légaré et al. 2004; Ménard et al. 2019; Henneb et al. 2019). These species may indirectly impede the restoration of caribou habitat by increasing the food availability for moose and bears (Bastille-Rousseau et al. 2011; Laurian et al. 2012; Lesmerises et al. 2015), thus resulting in higher mortality risks for caribou (Leblond et al. 2016; Mumma et al. 2018).

Deciduous stands in the vicinity of roads also influenced species establishment in our study by favoring the growth of raspberries, currants, and white birch. On seismic lines, van Rensen et al. (2015) found that the percentage of sites regenerated was higher in areas surrounded by young deciduous stands. Our study revealed that the presence of deciduous stands increased fruit-bearing shrubs and herbaceous species abundance, which, as mentioned before, could attract alternate prey and predators of caribou and increase caribou mortality risks.

Implications for boreal caribou conservation

In eastern Canada, boreal caribou are associated with mature coniferous forests dominated by black spruce (Hins et al. 2009; Ray 2014). As such, the restoration treatment that we deemed most favorable to boreal caribou was the combination of closing, decompacting, and planting. In these sites, the occurrence of black spruce was higher, and that of species competing with black spruce, i.e., herbaceous species, blueberries, and deciduous trees, lower. The addition of organic matter did not seem to be effective for spruce growth, and could even be counterproductive by slightly increasing the abundance of herbaceous species that can outcompete black spruce. Some species may benefit from the presence of herbaceous and deciduous trees (e.g. small mammals; Seccombe-Hett & Turkington 2008; Baltensperger et al. 2015), but our aim was to restore the habitat to its pre-disturbance condition, i.e., an environment less suitable to alternate prey and predators, and auspicious to the successful recovery of boreal caribou, a species threatened under the Canadian Species at Risk Act. Considering that late-successional forest species are often those that suffer most from intensive forest management practices (e.g., St-Laurent et al. 2008), such restoration efforts could also benefit other sensitive species of the boreal forest (see Bichet et al. 2016).

Ideally, the most suitable habitat for boreal caribou would be roadless (Vistnes & Nellemann 2008; Leblond et al. 2014). Needless to say, most roads are still used by humans, but in regions where road density can be reduced, the decommissioning of abandoned secondary roads has been shown to favour landscape connectivity for caribou (Bauduin et al. 2018). Our recommended treatment, i.e., closing the road, decompacting the soil, and planting 1,500 black spruce trees per linear km, cost ~2,175 $CAD/km in 2016. This cost could become prohibitive when applied at a very broad scale. To reduce costs, conservation efforts could be focused along known travel corridors used by caribou.

Our study presented the effects of treatments on vegetation only 3 to 4 years after road decommissioning, which means that the regeneration trajectory of plant communities could still change during the next 10–30 years, as succession proceeds and trees mature. For instance, natural regeneration of late-successional plants (such as bryophytes) and lichens was seldom visible shortly after restoration. Lichens are essential food items for caribou especially during late winter (Courbin et al. 2009; Ray 2014), but several studies have shown that terrestrial lichens can take as long as 60 years to regenerate post-disturbance, while arboreal lichen can take up to 90 years (Stone et al. 2008; Boudreault et al. 2015). Therefore, long-term monitoring will be required to ensure that lichens regenerate in decommissioned forest roads. Besides, we found that inter-site variability within a given treatment was often high, suggesting that environmental covariates constrained vegetation regeneration, possibly more so than treatments per se. These sites would need to be monitored regularly to ensure that they lead to suitable caribou habitat in the future. Furthermore, establishment of vegetation on decommissioned roads could vary across regions. For example, St-Pierre et al. (2021) showed that the number of degree-days influenced vegetation composition on naturally regenerated forest roads, and that roads abandoned recently were mainly colonized by deciduous species. Nevertheless, empirical evidence from Norway (for reindeer, another subspecies of caribou), where the removal of a ski trail allowed a population to return to its previously occupied area 10 years after habitat restoration (Nellemann et al. 2010), suggests that these types of management actions are worthwhile. Further studies will need to evaluate the medium- to long-term effects of road decommissioning on the suitability of caribou habitat, including their use by alternate prey and predators. Considering the urgent need to protect caribou and the time and financial investments needed to achieve efficient restoration of their habitat, managers may need to combine habitat restoration with other, more short-term conservation strategies (e.g., maternal penning, predator control, translocation; Johnson et al. 2019).

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SUPPORTING INFORMATION

Appendix 1.1: Plant species sampled during the study. The percentage of sampling sites with at least one stem or tussock of a given species or species group is indicated as occurrence (%). Species or species groups occurring in more than 20% of sampling plots were included in our analyses.

Species inclusion	**Species or species groups**	**Occurrence (%)**
Included	Graminoids	99.0
	Balsam fir (*Abies balsamea*)	93.1
	Pearly everlasting (*Anaphalis margaritacea*)	93.0
	Black spruce (*Picea mariana*)	92.1
	White birch (*Betula papyrifera*)	85.1
	Fireweed (*Chamerion angustifolium*)	70.3
	Hawkweed (*Hieracium* spp.)	66.3
	Raspberry (*Rubus* spp.)	58.4
	Trembling aspen (*Populus tremuloides*)	56.4
	Dwarf dogwood (*Cornus canadensis*)	53.5
	Blueberry (*Vaccinium* spp.)	53.5
	Willow (*Salix* spp.)	53.5
	Creeping snowberry (*Gaultheria hispidula*)	42.6
	Currant (*Ribes* spp.)	31.7
Excluded	Balsam poplar (*Populus balsamifera*)	18.8
	Wild lily-of-the-valley (*Maianthemum canadense)*	17.8
	Labrador tea (*Rhododendron groenlandicum*)	16.8
	Twinflower (*Linnaea borealis*)	14.9
	Horsetail (*Equisetum* spp.)	13.9
	Green alder (*Alnus alnobetula*)	10.9
	Sheep laurel (*Kalmia angustifolia*)	10.0
	Northern starflower (*Trientalis borealis*)	9.9
	Clubmoss (*Lycopodium* spp.)	5.9
	Red clover (*Trifolium pratense*)	4.0
	Ferns	3.0
	Round-leaved sundew (*Drosera rotundifolia*)	3.0
	Mountain ash (*Sorbus* spp.)	2.0
	Speckled alder (*Alnus incana*)	2.0
	Tufted vetch (*Vicia cracca*)	2.0

Appendix 1. 2: Mean ($\bar{X}$), standard deviation (SD), and range of the number of stems per 4-m2 plots and the number of plots with at least one stem (occurrence) of raspberry (*Rubus* spp.) or currant (*Ribes* spp.) in control roads (n=200) and treatments (closed [n=435], decompacted [n=438], planted [n=456] and enriched [n=451]).

Treatments	**Raspberry**			**Currant**		
	$\bar{X}$ ± SD	**Range**	**Occurrence**	**$\bar{X}$ ± SD**	**Range**	**Occurrence**
Controls	0.1 ± 0.5	0–5	3.5%	-		absent
Closed	0.9 ± 4.7	0–47	7.4%	0.1 ± 1.1	0–21	1.6%
Decompacted	1.1 ± 5.3	0–60	15.5%	0.0 ± 0.3	0–4	2.1%
Planted	2.1 ± 7.1	0–53	20.8%	0.1 ± 0.7	0–9	5.9%
Enriched	0.7 ± 2.5	0–21	16.6%	0.3 ± 1.3	0–16	7.3%

The occurrence and average abundance of raspberry and currant stems was higher in the three most intensive treatments, suggesting that decompacting and planting favored these fruit-bearing shrubs. Switalski and Nelson (2011) also found that fruit-bearing shrubs increased on gated, barriered, or recontoured roads in Idaho, USA. As demonstrated by Archambault et al. (1998) and Widen et al. (2018), once established, these species can persist for at least 10 years post-disturbance, which may delay spruce tree establishment, notably through competition for light.

Appendix 1.3: Eigenvalue, correlation, proportion explained, *F* and *P*-values of the first three axes of the partial canonical correspondence analysis (pCCA) relating the number of stems or tussocks of plant species (or species groups) present in more than 20% of sampling sites to treatments and environmental variables surrounding sampling sites on treated roads.

Axis	**Eigenvalue**	**Correlation**	**Proportion explained**	***F***	***P*-value**
CCA 1	0.12	0.84	0.25	29.72	0.01
CCA 2	0.03	0.65	0.05	6.00	0.10
CCA 3	0.01	0.55	0.03	3.42	0.77
Model				3.36	0.01

Appendix 1.4: Mean ($\bar{X}$), standard deviation (SD), range (min–max), chi-square (X^2), *F* and *P*-values of covariates used in the partial canonical correspondence analysis (pCCA) used to assess the number of stems or tussocks of plant species (or species groups) present in more than 20% of sampling sites.

Predictor variables	**$\bar{X}$ ± SD**	**Range**	**X^2**	***F***	***P*-value**
Treatments	–		0.13	7.15	0.01
Old clearcuts (%)	4.7 ± 9.4	0.0 – 65.3	0.01	2.83	0.04
Deciduous (%)	0.8 ± 3.3	0.0 – 28.5	0.01	2.15	0.08
Wetlands (%)	0.5 ± 1.5	0.0 – 6.9	0.01	1.36	0.21
Mixed (%)	1.4 ± 5.8	0.0 – 37.7	0.00	0.73	0.51
Coniferous (%)	17.1 ± 14.4	0.0 – 50.1	0.01	1.53	0.18
Natural disturbances (%)	14.4 ± 13.7	0.0 – 46.7	0.00	1.02	0.35
Road width (m)	4.2 ± 0.9	2.5 – 6.5	0.01	2.49	0.01
Slope (°)	14.0 ± 10.0	0.0 – 50.0	0.01	1.87	0.10
Road orientation (°)	181.0 ± 86.0	11.0 – 354.0	0.00	0.99	0.36

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CHAPITRE 2
FIN DE LA ROUTE : RÉPONSES À COURT TERME D'UNE COMMUNAUTÉ DE GRANDS MAMMIFÈRES AU DÉMANTÈLEMENT DES CHEMINS FORESTIERS

2.1 RÉSUMÉ EN FRANÇAIS DU DEUXIÈME ARTICLE

Les perturbations humaines augmentent à l'échelle mondiale, causant la perte, l'altération et la fragmentation des habitats fauniques. Au Canada, le démantèlement des structures linéaires a été identifié comme outil prometteur pour restaurer l'habitat des populations menacées du caribou boréal (*Rangifer tarandus caribou*) en diminuant les ressources alimentaires pour les proies alternatives et en diminuant les probabilités de rencontre entre le caribou et ses prédateurs. Dans cette étude, nous avons examiné l'utilisation de 40 km de chemins forestiers démantelés par les caribous, les loups (*Canis lupus*), les ours (*Ursus americanus*) et les orignaux (*Alces americanus*), 1–3 années après leur démantèlement, en utilisant 232 caméras automatisées. Nous avons comparé quatre traitements additifs : fermer l'accès du chemin aux humains, décompacter le sol, planter des épinettes noires (*Picea mariana*) et ajouter du sol enrichi. Nous avons évalué l'influence des traitements, de l'utilisation faite par les autres mammifères et de l'environnement adjacent aux chemins sur l'utilisation des chemins par les quatre espèces. Les caribous utilisaient les traitements plantés plus que les chemins fermés (référence), mais les traitements n'ont pas influencé l'utilisation des chemins démantelés par les ours et les orignaux. Nous n'avons pas pu évaluer l'utilisation des chemins par les loups en raison de la faible taille de l'échantillon. L'utilisation des chemins démantelés par les caribous diminuait avec l'augmentation de la densité locale d'orignaux, mais augmentait avec de fortes densités locales d'ours. Les caribous ont été observés plus souvent sur les chemins adjacents à des forêts matures ou en

régénération résineuse; les caribous ont également utilisé davantage les chemins adjacents à des milieux humides. Nos résultats suggèrent que le traitement combinant la fermeture, la décompaction et la plantation pourrait être bénéfique pour les caribous, soulignant la pertinence d'appliquer des efforts de restauration active dans les programmes de conservation des populations de caribous. Nous recommandons que la fermeture, la décompaction et la plantation soient ajoutées aux protocoles de démantèlement pour la conservation des espèces en péril, parallèlement à la protection des habitats à grande échelle.

J'ai rédigé ce deuxième article, intitulé « *End of the road: Short-term responses of a large mammal community to forest road decommissioning* », en collaboration avec mon directeur Martin-Hugues St-Laurent, professeur en écologie animale à l'Université du Québec à Rimouski, et mon codirecteur Mathieu Leblond, chercheur scientifique à Environnement et Changement climatique Canada. Cet article a été soumis en octobre 2021 dans le *Journal for Nature Conservation*, une revue scientifique internationale à comité de révision par les pairs. En tant que première auteure, j'ai contribué à cet article par la gestion des données récoltées sur le terrain par nos collaborateurs du Conseil de la Première Nation des Innus Essipit. J'ai réalisé l'ensemble des analyses statistiques et géomatiques, ainsi que mené l'écriture et la révision de l'article. Mes co-auteurs ont, en plus d'avoir supervisé l'étude et coordonné le financement, participé à l'écriture et la révision du manuscrit. Les résultats de ce deuxième article ont été présentés lors du *9th World Conference on Ecological Restoration* (SER) en juin 2021 et au congrès de la Société Québécoise pour l'Étude Biologique du Comportement (SQÉBC) en novembre 2021.

2.2 End of the road: Short-term responses of a large mammal community to forest road decommissioning

Abstract

Anthropogenic disturbances are increasing worldwide, causing wildlife habitat loss, alteration, and fragmentation. In Canada, the decommissioning of linear anthropogenic structures was identified as a promising tool to restore the habitat of threatened populations of boreal caribou (*Rangifer tarandus caribou*) by reducing food availability for alternate prey and decreasing encounter probabilities with predators. In this study, we monitored the use of 40 km of decommissioned forest roads by caribou, gray wolves (*Canis lupus*), black bears (*Ursus americanus*), and moose (*Alces americanus*) 1–3 years after reclamation, using 232 motion-activated camera traps. We compared four additive treatments: closing the road to human access, decompacting its soil, planting black spruce (*Picea mariana*) trees, and adding enriched soil. We assessed the influence of treatments, use by other large mammals, and characteristics of the surrounding environment on road use by the four species. Caribou used the planted treatment more than the closed (reference) treatment, but treatments did not influence the use of decommissioned roads by bears and moose. We could not assess the use of roads by wolves because of low sample size. Road use by caribou declined with local moose density, but increased with local bear density. Caribou were observed more frequently on roads surrounded by regenerating and mature coniferous stands; caribou also preferentially used roads surrounded by wetlands. Our results suggest that the treatment combining road closure, soil decompaction, and tree planting could be beneficial to caribou, highlighting the relevance of applying active restoration protocols in caribou conservation programs. We recommend road decommissioning be added to the toolbox of land managers for the conservation of species at risk, alongside broad-scale habitat protection.

INTRODUCTION

Anthropogenic disturbances can induce the loss, alteration, and fragmentation of wildlife habitat, and are identified as one of the main drivers of the contemporary biodiversity "crisis" (Maxwell et al., 2016; WWF, 2020). Disturbances can threaten whole ecosystems through their negative impacts on wildlife behavior, physiology, demography, and even community composition (Johnson and St-Laurent, 2011). The community-level impacts of human disturbances can be complex. For instance, by improving growth rates of competitors and predators, human features can destabilize predator-prey relationships and induce the decline of prey through apparent competition (Holt, 1977). Such anthropogenically enhanced predation pressure is believed to be the main cause of decline for most boreal populations of woodland caribou (*Rangifer tarandus caribou*; hereafter boreal caribou) across Canada (Wittmer et al., 2007). Increased predation from both gray wolf (*Canis lupus*) and black bear (*Ursus americanus*), and subsequent population declines, have led to the designation of boreal caribou as threatened under the Species at Risk Act (SC, 2002). Conservation of this species is believed to be largely dependent on the protection of old-growth boreal forests and vast, pristine areas (Ray, 2014).

Timber harvesting is a major disturbance of the Canadian boreal forest. The conversion of old-growth black spruce forests favored by boreal caribou (Courbin et al., 2009; Ray, 2014) into young deciduous stands suitable to other cervids like moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*; Potvin et al., 2005; Bowman et al., 2010) can set the stage for apparent competition to occur (Wittmer et al., 2007). Growing populations of alternate prey can support greater gray wolf populations, thereby increasing predation risk on caribou (Latham et al., 2011). The increase in forage availability in harvested areas is also profitable to black bears (Mosnier et al., 2008; Dussault et al., 2012), which are opportunistic but efficient predators of caribou calves and can affect caribou recruitment (Bastille-Rousseau et al., 2011; Leclerc et al., 2014). The road network associated with timber harvesting can also increase food availability for alternate prey (Laurian et al., 2012) and facilitate the movements of predators (Tigner et al., 2014; Dickie et al., 2017a), resulting in a higher encounter rate with caribou (Whittington et al., 2011;

Mumma et al., 2018) including in suitable caribou habitats such as wetlands (Ray, 2014; Mumma et al., 2019). Despite ample empirical evidence showing that anthropogenic disturbances can contribute to decreased boreal caribou population growth rates (e.g., Environment Canada, 2012; Rudolph et al., 2017), most jurisdictions are only beginning to consider habitat restoration (and notably the decommissioning of linear features) as a promising avenue to reduce the influence of human disturbances on boreal caribou (e.g., Johnson et al., 2019).

Throughout the last decade or so, studies on the restoration and reclamation of linear features have shown that vegetation cover could impede the movements of the main predators of caribou (Tigner et al., 2014; Dickie et al., 2017b), and some restoration projects have used this knowledge to reduce predation risks, e.g. by adding large obstacles such as logs onto seismic lines (Keim et al., 2019). Although these approaches can reduce the ability of predators to travel on linear features, they are not meant to restore vegetation communities to pre-disturbance conditions, which may be necessary for caribou recovery. To achieve this goal, long-term restoration practices may be required (Environment Canada, 2012; Ray, 2014). Passive restoration, where vegetation is left to grow naturally, has the advantage of being relatively inexpensive, but may sometimes leave an important proportion of linear features with no vegetation or with a regrowth composed of deciduous species rather than coniferous trees (Lee and Boutin, 2006; St-Pierre et al., 2021). This may benefit wolves, bears and moose more so than caribou (e.g., Finnegan et al., 2018). On the other hand, active restoration, while being costlier, has a greater potential to lead to suitable habitat (e.g., Tarvainen and Tolvanen, 2016) through mechanical site preparation or the planting of seeds or trees to speed up vegetation recovery and guide regeneration trajectories (e.g., Dickie et al., 2021; Lacerte et al., 2021).

Forest roads are the most prevalent linear disturbance type found in eastern Canada (Pasher et al., 2013). Contrary to western Canada, this region is virtually devoid of seismic lines. Forest roads differ from seismic lines in terms of line characteristics, size and function (Desautels et al., 2009; Pasher et al., 2013; Dabros et al., 2018), meaning that large-mammal reactions observed in oil-and-gas-dominated landscapes may differ from those found in timber-harvest-dominated landscapes (Dickie et al., 2017a; Tattersall et al., 2020). On decommissioned forest roads, Lacerte et al. (2021) suggested that closing a road to traffic, decompacting its soil and planting black spruce (*Picea mariana*) trees should provide regeneration conditions that are most likely to lead to suitable caribou habitat, and less likely to favor predators and alternate prey; however, they did not assess the response of large mammals to these treatments. Several authors, such as Tattersall et al. (2020) who found that animals did not only respond to treatment types but also to the surrounding environment, measured the response of large mammals to habitat restoration on seismic lines, but few studies have evaluated these responses on roads. Therefore, the empirical response of large mammals to active forest road decommissioning remains largely unknown.

In this study, we examined the use of decommissioned forest roads by boreal caribou, gray wolves, black bears, and moose, 1 to 3 years following treatments aimed at restoring suitable habitat for caribou. These treatments were designed to promote natural vegetation regeneration that would ultimately obstruct predator movements as well as lead to the establishment of a mature coniferous cover typical of suitable boreal caribou habitat (Leblond et al., 2014; Ray, 2014). Treatments consisted in (1) closing the road to human circulation, (2) closing and decompacting the road to promote natural regeneration, (3) closing and decompacting the road, and planting black spruce trees, and (4) closing and decompacting the road, planting trees, and enriching the soil with organic matter (see *2.2 Road-decommissioning treatments* for details). Our objective was to measure the influence of incremental restoration efforts (decompaction, tree planting, and enrichment) on the occurrence and frequency of use of decommissioned forest roads by caribou, wolves, bears, and moose shortly after road decommissioning. In a companion study, we found that vegetation establishment on the same decommissioned roads varied across treatments (Lacerte et al. 2021), with closed, decompacted, and enriched roads favoring the regeneration of plant species preferred by bears and moose (i.e., herbaceous plants, deciduous trees, fruit-bearing shrubs) and planted roads favoring the regeneration of black spruce, thereby benefiting caribou. In view of these results, we hypothesized that resource availability (i.e., vegetation for herbivores, prey for carnivores, both for omnivores) on forest roads or in the surrounding environment, as well as predation risk for prey, would influence the use of decommissioned forest roads by the large mammal community. We predicted that use of roads by caribou would increase with restoration intensity, especially on planted treatments as this treatment was shown to provide regeneration conditions suitable to caribou and less suitable to its predators (Lacerte et al., 2021); we predicted the opposite for wolves, bears, and moose. We also predicted that road use by caribou would decrease with the intensity of use by predators and alternate prey, and that road use by predators would increase with the availability of their prey. Finally, we predicted that the environment surrounding decommissioned forest roads would influence road use by mammals, with coniferous stands and wetlands being used more by caribou (Ray, 2014) and recent clearcuts and deciduous stands being used more by wolves, bears, and moose (Bowman et al., 2010; Latham et al., 2011; Dussault et al., 2012).

METHODS

Study area

The study area was located in the projected biodiversity reserve Akumunan, in the traditional territory of the Essipit First Nation to the northeast of the Saguenay River in Québec, Canada (70° 08′ W, 48° 44′ N; Figure 2.1). The 285 km^2 area was part of the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain, and had a subarctic humid continental climate (Robitaille and Saucier, 1998). Throughout the study period (May – September), mean temperature and mean precipitation were respectively 14.7 °C and 88.4 mm (Environment Canada, 2020). The study area was located at the southern fringe of the continuous distribution of boreal caribou in Québec, where caribou were found at a density of 0.6/100 km^2 (Plourde et al., 2020). The only major predators of caribou in the study area were gray wolves and black bears. No wolf density estimates were available for this specific study area, but Jolicoeur (1998) reported a density of 0.4 wolves/100 km^2 close to our study area (~185 km southwest). This density is equal to the lowest estimate found in other regions where use of roads by wolves was recently studied (e.g., 0.4-1.5/100 km^2 in western Canada; Kuzyk and Hatter, 2014), and could be explained by the intensive harvesting exerted by local trappers. Bears and moose were found at densities of 0.4-1.3/10 km^2 (MFFP, unpublished data) and 2.4/10 km^2 (Ayotte and Chenel, 2019), respectively.

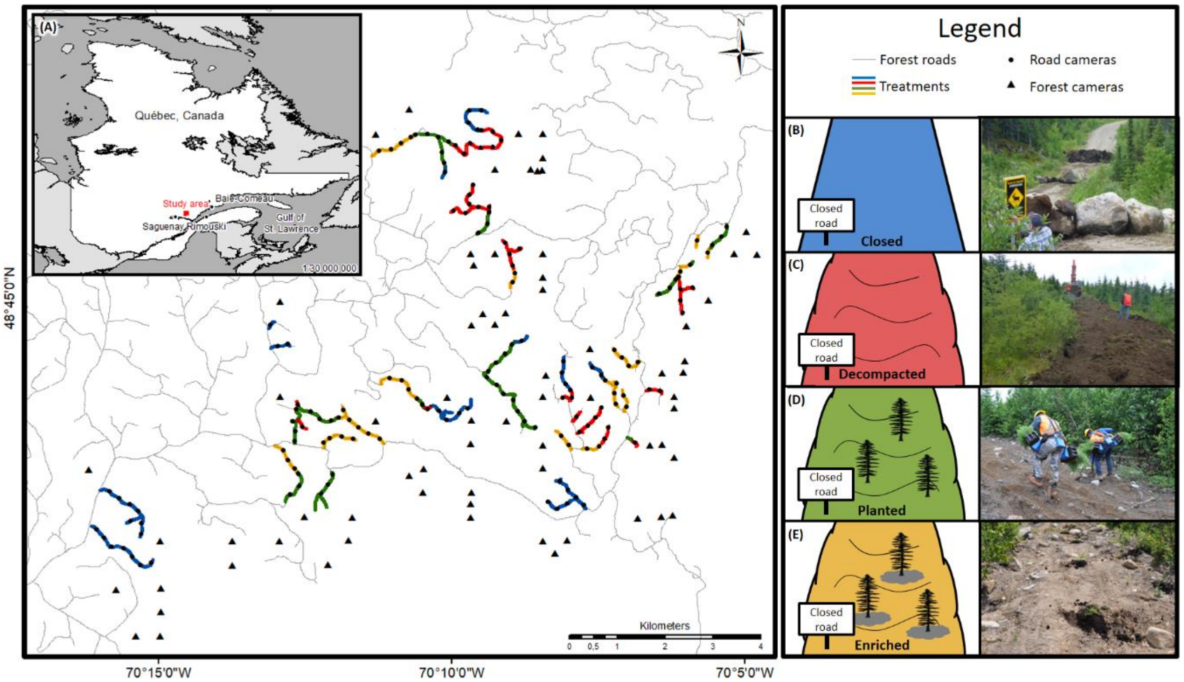

Figure 2.1: *On the left* – Study area located in the projected biodiversity reserve Akumunan, in the traditional territory of the Essipit First Nation to the northeast of the Saguenay River in Québec, Canada. Motion-activated cameras were placed along 40 km of decommissioned forest roads (black dots, called road cameras, n = 161) and in the surrounding environment (black triangles, called forest cameras, n = 71). *On the right* – The four forest road decommissioning treatments are illustrated: closed (B), decompacted (C), planted (D), and enriched (E).

Road-decommissioning treatments

We compared four road decommissioning treatments distributed across 40 km of roads abandoned by the timber harvesting industry over the last 20 years. We recently assessed the establishment of vegetation on these roads (Lacerte et al., 2021). Treated road segments were usually 1 km in length and were distributed randomly throughout the study area. Each of the four road treatments was performed over a total of approximately 10 km. The Essipit First

Nation conducted the decommissioning operations in 2015 and 2016. In the first treatment, road segments were closed to human circulation by placing large boulders, digging trenches, creating obstacles with the removed material, and adding a sign indicating that the road was closed (hereafter the closed treatment; Figure 2.1b). Roads were also closed in the second treatment, and the soil was decompacted at a depth of 30 to 40 cm using an excavator while preserving the natural regeneration of coniferous trees whenever possible (hereafter the decompacted treatment; Figure 2.1c). In the third treatment, in addition to closing and decompacting the road, 1500 black spruce stems per linear km were planted (hereafter the planted treatment; Figure 2.1d). In the fourth treatment, all of the above were combined with the addition of organic matter (garden soil) at the base of each planted tree (hereafter the enriched treatment; Figure 2.1e). Across planted and enriched treatments, a total of 30 000 spruce trees were planted during the summer of 2016. Planted stems were on average 30 cm in height.

Use by animals

We evaluated use of decommissioned forest roads by caribou, wolves, bears and moose by installing 161 motion-activated cameras (Stealth Cam PX12FX) along treated road segments during the summers of 2017 and 2018 (322 camera-years). Cameras were distanced by ~250 m, for a total of 4 cameras per km (hereafter "road cameras"). To control for the effect of changes in local density of mammals across years on road use, we also installed 71 additional cameras (141 camera-years) in the surrounding environment, at least 250 m away from a road but no farther than 1 km (hereafter "forest cameras"). These cameras were distributed randomly across our study area but were distanced by a minimum of 500 m, for a final density of 2.25 cameras/km^2. Cameras were active between early July – August and October, thus covering most of the period during which caribou calves are highly vulnerable to predation by bears, and to a lesser extent by wolves (early June to late September: Leclerc et al., 2014). We used the number of active camera-days as a proxy of sampling effort; cameras with a sampling effort < 14 were removed from our analysis (15 camera-years; 3.2 %).

We used the software Timelapse2 (Greenberg, 2021) to analyze photos. We observed photos of the four large mammal species and counted the number of events per camera. Similar to Keim et al. (2019), the number of events reflected the number of individuals on a given photo (e.g., two wolves on one photo = two events). As individual recognition was often impossible, we considered all observations within a 30 min interval as one event to avoid counting one individual moving in front of the camera during a short period of time as multiple events (similar to Rovero and Zimmermann, 2016). We generated an index of the intensity of use for each species (no. of events per 100 days) for both road and forest cameras (sensu Keim et al., 2019). We used the intensity of use for forest cameras as a proxy of the local density of species surrounding roads (hereafter local density). We interpolated local densities using a Triangular Irregular Network across the study area (Li and Heap, 2008). We then used this model to link local animal densities to each road camera in ArcGIS v.10.3 (ESRI, 2018). We were unable to interpolate local densities for 7 road cameras because they were found outside of the interpolated network; these were removed from the analysis (2.2 % of road camera-years).

Environmental covariates

We generated five land cover types within a geographic information system in ArcGIS v.10.3 (ESRI, 2018): (1) deciduous forests, (2) wetlands, (3) natural disturbances (fires, windthrows and insect epidemics), (4) recent clearcuts (≤ 20 years old), and (5) regenerating and mature coniferous forests (> 20 years old, up to 120 years old). We obtained those using a reclassification of 1 : 20 000 digital maps provided by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) and updated annually (minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas). We calculated the percentage of each land cover type within 250 m, 500 m and 1 km buffer radii centered on each camera. We also determined road density (km/km^2) within the same buffers using all primary and secondary roads included in the Routard 1 : 20 000 numerical maps published by the MFFP. We generated principal coordinates of neighbour matrices (PCNM; see Borcard and Legendre, 2002) for each species to account for spatial autocorrelation in our study design. PCNMs are a spectral decomposition of the spatial relationships among sampling sites, which generates variables corresponding to all relevant spatial scales in a dataset (Borcard et al., 2004). For each species separately, we retained the PCNMs that had a statistically significant (*P*-values ≤ 0.05) effect on the spatial structure of the frequency of use of decommissioned forest roads (following St-Pierre et al. submitted; see Appendix 2.1).

Statistical analyses

For the purposes of our statistical analyses, we combined variables into five distinct groups. We first combined the intensity of decommissioned road use by caribou, wolves, bears and moose into the "road use" group (estimated using the "road cameras"), and the local densities of caribou, bears and moose into the "local density" group (estimated using the "forest cameras"). Wolves were never observed by forest cameras; we were thus unable to generate a local density estimate for this species. We included wetlands, deciduous forests, and coniferous forests into the "undisturbed land cover" group, and natural disturbances, recent clearcuts, and road density into the "disturbed land cover" group. The final group included the significant PCNMs (see Appendix 2.1). We selected the most parsimonious buffer radii for undisturbed and disturbed land cover groups by ranking them using Akaike's information criterion corrected for small sample sizes (AIC_c; see Malcolm et al., 2020). The best (i.e., most parsimonious) buffer sizes to explain variations in use of road segments by large mammals differed among land cover groups and species (see Appendix 2.2); we only used these best buffer sizes in subsequent analyses.

We used generalized linear mixed models to assess the influence of covariates on the use of decommissioned forest roads by caribou, bears, and moose. We could not assess the use of roads by of wolves because of low sample size and a skewed distribution of absences across treatment types, as wolves were never observed on enriched treatments. Due to the high number of null values in our data (i.e., many camera-years had no photo for a given species), we used hurdle models (see e.g., Lesmerises et al., 2013), which are better at handling zero-inflated data sets than other distributions such as Poisson. We first evaluated the occurrence, i.e., the presence or absence of a species at a road camera during the whole study period, using mixed logistic regression models (hereafter the “occurrence” models). For the second part of the hurdle model, we only kept presences and assessed the extent of road use by the three species using mixed negative binomial models. We attempted using the intensity of use (no. of events per 100 days; sensu Keim et al., 2019), but we had to use the raw number of events (or frequency of use; sensu Dickie et al., 2021) instead due to convergence problems (hereafter the “frequency of use” models). We included the sampling effort (no. of active camera-days) as a covariate in “occurrence” models, and as an offset in “frequency of use” models to control for the variable detection rates among cameras.

For both occurrence and frequency of use models, we built 15 candidate models that represented a priori biological hypotheses (Table 2.1). These models combined the 5 groups of variables presented earlier. Road decommissioning treatments were included in all models because our main objective was to evaluate the effect of incremental restoration efforts on the use of decommissioned forest roads by large mammals. In each model, we included the road segment ID as a random effect, and the local density of the focal species as a covariate to control for changes in species density across years. We used the same basic model structures for the three mammal species but slightly adjusted model composition to match each species’ ecology (see Appendix 2.3).

Some models caused convergence issues and had to be dropped. We used the Variance Inflation Factor (VIF) to diagnose multicollinearity problems; VIF values were ≤ 4.3. We verified model assumptions by assessing deviations from the expected distribution and comparing the standardized residuals and predicted values (Hartig, 2020). Models that did not meet assumptions were removed from the list of candidate models. We ranked candidate models using AIC_c and interpreted the most parsimonious model only (Burnham and Anderson, 2001; Table 2.1). We assessed model fit using the area under the Receiver Operating Characteristic curve (AUC) for “occurrence” models and the marginal R^2 for “frequency of use” models. We determined the fit as good (AUC > 0.80; $R^2 > 0.60$), moderate (AUC of 0.65 to 0.80; R^2 of 0.25 to 0.60), or low (AUC < 0.65; $R^2 < 0.25$). Finally, we considered β with 95 % CI excluding 0 as statistically significant for "occurrence" and "frequency of use" models. We conducted all analyses using R v.3.5.1 (R Core Team, 2018).

Table 2.1: Candidate models used to assess variations in the occurrence (Occ.; logistic regression) and frequency of use (Freq.; binomial negative) of decommissioned forest roads by boreal caribou, black bear, and moose. We present each model with its number of parameters (k) and ΔAIC_c i.e., the difference between the model and the most parsimonious model. Retained models are indicated in bold. Models which caused convergence issues or models that did not meet assumptions and had to be dropped are indicated using –.

Model		**Boreal caribou**				**Black bear**				**Moose**			
		Occ.		**Freq.**		**Occ.**		**Freq.**		**Occ.**		**Freq.**	
		k	**ΔAIC_c**	**k**	**ΔAIC_c**	**k**	**ΔAIC_c**	**k**	**ΔAIC_c**	**k**	**ΔAIC_c**	**k**	**ΔAIC_c**
1	Treatments	7	35.18		–	7	1.55		–		–	7	1.07
2	T + Other species	9	31.63		–	**9**	**0.00**		–		–	**9**	**0.00**
3	T + Local density	9	20.19	9	0.20	9	5.67	9	0.84		–	8	2.33
4	T + Undisturbed	9	21.66	**9**	**0.00**	9	3.18	**9**	**0.00**	8	7.14	9	4.32
5	T + Disturbed	10	30.35	10	5.82	10	4.02	10	4.85	9	2.27	10	5.81
6	T + PCNM	18	51.85		–	12	4.91	12	12.24		–	14	10.95
7	T + Species + Undisturbed	11	15.78		–	11	2.75		–		–	11	3.21
8	T + Species + Disturbed	12	26.50		–	12	1.52		–	**11**	**0.00**	12	4.70
9	T + Species + PCNM	20	47.03		–	14	2.97		–		–	16	12.19
10	T + Local + Undisturbed	**11**	**0.00**	11	5.46	11	7.39		–	9	9.15	10	5.75
11	T + Local + Disturbed	12	15.87	12	13.25	12	8.05	12	7.90	10	4.37	11	7.57
12	T + Local + PCNM	20	40.13		–	14	9.26	13	12.14		–	15	11.57
13	T + Undisturbed + Disturbed		–	11	8.21	11	5.97		–	11	1.27	12	9.52
14	T + Undisturbed + PCNM	20	40.24		–	14	7.42	14	13.53		–	16	14.84
15	T + Disturbed + PCNM	21	48.21		–	15	7.17	15	20.61		–	17	14.85

RESULTS

Our sampling effort totaled 21 363 road camera-days (n = 298 road camera-years from 149 road cameras) and 11 205 forest camera-days (n = 141 forest camera-years from 71 forest cameras). Moose were the most detected species on road cameras with a total of 596 events, followed by bears (106), caribou (76), and wolves (11). Moose were also the most detected species on forest cameras (95 events), followed by caribou (27), and bears (5). Wolves were not detected on forest cameras.

Boreal caribou

The most parsimonious model explaining variations in the occurrence of caribou on decommissioned forest roads included local densities of bears and moose, and the undisturbed land cover group (model M10; Table 2.1). This model had a good fit (AUC = 0.93; Table 2.2). The probability that a caribou used a given decommissioned road increased with local density of bears and the proportion of regenerating and mature coniferous stands, and decreased with local density of moose. The frequency of use by caribou was best explained by a model composed of the undisturbed land cover group (M4; Table 2.1). The model had a moderate fit to the data (R^2 = 0.50; Table 2.2). The frequency of use by caribou was higher on planted roads compared to closed roads, and was positively related to the proportion of coniferous forests and wetlands in the surrounding environment.

Table 2.2: Most parsimonious models explaining the variation in occurrence (Occ.; logistic regression) and frequency of use (Freq.; binomial negative) of decommissioned forest roads by boreal caribou, black bear, and moose. We present each covariate with its parameter estimate (β) and 95% confidence intervals (95% CI; [Lower: Upper]). Closed roads were used as the reference treatment. Variables with a 95% CI not overlapping zero were considered as statistically significant and are indicated in bold.

Variables	Boreal caribou				Black bear				Moose			
	Occurrence		Frequency		Occurrence		Frequency		Occurrence		Frequency	
	β	95% CI	β	95% CI	β	95% CI	β	95% CI	β	95% CI	β	95% CI
Intercept	**-4.55**	**[-6.48: -2.61]**	**-4.27**	**[-5.16: -3.38]**	**-1.82**	**[-2.58: -1.07]**	**-3.72**	**[-4.19: -3.24]**	0.60	[-0.06: 1.13]	**-3.02**	**[-3.28: -2.76]**
Treatments												
Decompacted	0.54	[-1.24: 2.32]	0.91	[-0.10: 1.93]	0.35	[-0.63: 1.33]	0.26	[-0.34: 0.86]	-0.15	[-0.87: 0.58]	-0.15	[-0.52: 0.21]
Planted	0.30	[-1.50: 2.10]	**1.38**	**[0.40: 2.37]**	0.78	[-0.21: 1.76]	-0.12	[-0.71: 0.48]	-0.03	[-0.77: 0.71]	-0.38	[-0.77: 0.00]
Enriched	-1.36	[-3.41: 0.69]	0.95	[-0.36: 2.25]	-0.20	[-1.22: 0.82]	-0.32	[-1.06: 0.41]	0.01	[-0.73: 0.75]	-0.05	[-0.42: 0.32]
Other species												
Use by caribou		–		–	**0.31**	**[0.03: 0.59]**		–		–		–
Use by wolf		–		–		–		–	0.25	[-0.21:0.71]	**0.10**	**[0.01: 0.20]**
Use by bear		–		–		–		–	0.31	[-0.04:0.66]	-0.00	[-0.11: 0.11]
Use by moose		–		–	0.12	[-0.19: 0.44]		–		–		–
Local bear density	**0.90**	**[0.23: 1.57]**		–		–		–		–		–
Local moose density	**-4.91**	**[-8.80: -1.02]**		–		–		–		–		–
Land cover types [a]												
Wetland	-1.58	[-3.20: 0.05]	**1.09**	**[0.10: 2.08]**		–	**0.19**	**[0.01: 0.37]**		–		–
Deciduous forest		–		–		–	-0.16	[-0.42: 0.10]		–		–
Coniferous forest	**1.44**	**[0.75: 2.12]**	**0.63**	**[0.32: 0.94]**		–		–		–		–
Natural disturbances		–		–		–		–	**0.37**	**[0.04: 0.71]**		–
Recent clearcuts		–		–		–		–	0.28	[-0.00: 0.57]		–
Road density		–		–		–		–	**-0.32**	**[-0.59: -0.06]**		–
Concomitant variables												
Local caribou density	**1.05**	**[0.45: 1.66]**	**-0.97**	**[-1.97: -0.02]**		–		–		–		–
Local bear density		–		–	-0.13	[-0.47: 0.22]	0.00	[-0.20: 0.21]		–		–
Local moose density		–		–		–		–		–	-0.07	[-0.22: 0.07]
Sampling effort	-0.31	[-0.96: 0.35]		Offset	0.29	[-0.03: 0.61]		Offset	0.24	[-0.01: 0.49]		Offset
Road segment ID	0.76	NA	0.00	NA	0.37	NA	0.00	NA	0.09	NA	0.23	NA
Model fit												
AUC		0.93		–		0.70		–		0.66		–
R^2 marginal		–		0.50		–		0.17		–		0.08

[a]Caribou: measured within a 1 km buffer radius; Bear: 250 m buffer radius; Moose: 250 m buffer radius. See Appendix 2.2.

Black bear

Variations in the occurrence of black bears on decommissioned forest roads were best explained by road use by caribou and moose (M2; Table 2.1). This model had a moderate fit (AUC = 0.70) and suggested that the presence of bears was positively related to the intensity of use by caribou (Table 2.2). The frequency of use by bears was best explained by a model including the undisturbed land cover group (M4; Table 2.1), but the fit of this model was low ($R^2 = 0.17$; Table 2.2). This model suggested that the frequency of use by bears was positively related to the proportion of wetlands in the surrounding environment.

Moose

The most parsimonious model explaining variations in the occurrence of moose combined road use by wolves and bears, and the disturbed land cover group (M8; Table 2.1). This model had a moderate fit (AUC = 0.66) and showed that the presence of moose was positively related to the proportion of natural disturbances in the surrounding environment, and negatively related to road density (Table 2.2). Recent clearcuts had a marginally significant effect (based on an asymmetric 95 % CI vs. zero; Table 2.2). This effect could suggest that moose occurrence increased on decommissioned roads surrounded by a higher proportion of recent clearcuts. The model including road use by wolves and bears (M2; Table 2.1) was the best to explain variations in the frequency of use by moose, but its fit was low ($R^2 = 0.08$; Table 2.2). This model suggested that the frequency of use by moose was positively related to the intensity of use by wolves (Table 2.2).

DISCUSSION

Few studies have assessed the response of large mammals to decommissioned forest roads, the main type of linear disturbances in eastern Canada (Pasher et al., 2013). We partially filled this gap by identifying the determinants of use of decommissioned forest roads by boreal caribou, black bears, and moose, including the influence of incremental restoration efforts. Using a large network of automated camera traps distributed across a gradient of restoration treatments, we found that, globally, use of decommissioned forest roads was best explained by the level of use made by other large mammals and variables describing the environment surrounding treated road segments.

Effect of road decommissioning treatments

Road decommissioning treatments, used as a categorical variable (with four levels representing the four treatments), were mostly insufficient to explain variations in the use of decommissioned roads by the large mammal species found in our study area. In fact, they were only retained in models explaining the use of roads by caribou, with caribou use being higher on planted treatments compared to closed roads. This result supports findings from a companion study, where we assessed the effects of the same treatments on vegetation structure and composition (Lacerte et al., 2021). In this study, vegetation on the planted treatment appeared less attractive to predators and alternate prey, suggesting a lower predation risk for caribou. Dickie et al. (2021) found differences in the occurrence of caribou (and a non-significant trend on their frequency of use) across various treatments of differing intensity on seismic lines. They also found that frequency of use by wolves and moose declined with restoration intensity. In contrast, Tattersall et al. (2020) did not observe significant responses by caribou, gray wolves, black bears and moose to active restoration treatments, again on seismic lines. In contrast with studies conducted in western Canada, we were unable to assess wolf responses to treated forest roads due to low sample sizes (no. of photos) and the absence of wolves detected on the enriched treatment (see Appendix 2.4), a situation potentially explained by the low wolf densities resulting from the intensive trapping pressure in our study area. Also, we found no significant difference in the use of decommissioned forest roads by moose across treatments. However, we noted a non-significant trend suggesting that moose used planted treatments less than others (2.05 vs. ≥ 2.73 events/100 camera-days; see Appendix 2.4), which might be explained by the less attractive vegetation found on planted treatments (Lacerte et al., 2021). A study conducted in Idaho, USA, found that black bears used recontoured (decompacted) roads more than gated or barriered roads because of higher food availability (Switalski and Nelson, 2011). We noted a similar, albeit non-significant trend, with bears using decompacted roads more than the other three treatments (0.72 vs. ≤ 0.59 events/100 camera-days; see Appendix 2.4). Food availability was generally higher on decompacted roads (Lacerte et al., 2021), which might explain their slightly superior use by bears.

Effect of the intensity of road use by other large mammals

Our results showed that the use of decommissioned forests roads and local densities of other species influenced the occurrence and frequency of use by large mammals, more so than treatments per se. For instance, we found that the occurrence of caribou decreased with increased use by moose. Caribou are known to avoid moose habitat in order to avoid wolves, their shared predator (e.g., James et al., 2004; Peters et al., 2013). We were not able to assess the direct relationship between caribou and wolves due to low sample sizes for wolves (too few photos on roads), but considering that the frequency of moose increased with higher road use by wolves, it is likely that the habitat use tactic shown by caribou in our study also allowed them to avoid wolves. In regions where moose are more abundant than caribou (such as our study area), wolves concentrate their search image on moose, their main prey (Kittle et al., 2017). Moreover, other types of prey are readily available during the summer season (such as beaver *Castor canadensis*; Latham et al., 2011), making wolves less obligate to feed on ungulates, a result also confirmed by scat analyses (Tremblay et al., 2001). Therefore, our results may illustrate the typical “spacing away” anti-predation strategy used by caribou to avoid encountering wolves (e.g. Seip, 1992; James et al., 2004).

In stark contrast, we found that the occurrence of caribou increased with higher local bear density – another important predator of caribou – and that the occurrence of bears increased with higher decommissioned road use by caribou. In a study area close to ours (~185 km southwest), Leblond et al. (2016) showed that avoidance of wolves by caribou resulted in higher selection of areas suitable to bear. Moreover, bears in the same area tended to move frequently between vegetation-rich feeding sites, increasing the probability of encounter with (and predation on) caribou (Bastille-Rousseau et al., 2011). Therefore, similar to other boreal caribou populations in south-central Québec, it is possible that avoidance of wolves by caribou in our study area drove them closer to areas (and roads) used by bears, increasing their risk of predation.

Effect of the environment surrounding decommissioned forest roads

Variables characterizing the environment surrounding decommissioned forest roads were good predictors of the occurrence and frequency of use by caribou. They were also useful predictors of the occurrence of moose and the frequency of use by bears. Use of decommissioned roads by caribou increased with the proportion of coniferous stands and wetlands surrounding the area. This was not surprising, as mature coniferous forest stands and wetlands are preferential habitat of caribou (Hins et al., 2009; Ray, 2014). However, the frequency of use by bears was also positively related to the availability of wetlands. DeMars and Boutin (2018) and Mumma et al. (2019) found that linear structures in western Canada promoted predator access to wetlands, thereby reducing the spatial refuge of caribou in wetlands and increasing predation risk (James et al., 2004). This result, along with our finding that bear occurrence increased in areas used by caribou, suggests that roads surrounded by wetlands may represent areas of high predation risk.

The presence of moose increased with the proportion of natural disturbances and tended to increase with recent clearcuts, as observed in other studies (e.g., Peters et al., 2013; Finnegan et al., 2019). This result may be related to the abundant foraging opportunities found by moose in cutblocks adjacent to decommissioned roads. Mumma et al. (2021) found that moose selected 9– to 24-year-old clearcuts because they provided high-quality forage (Potvin et al., 2005). The presence of moose near regenerated areas post-disturbance could also attract wolves, and indirectly increase predation risk for caribou (Bowman et al., 2010; Peters et al., 2013).

Limits and scope

We assessed the utility of increasing restoration efforts when decommissioning forest roads to influence habitat use by a large mammal community, but only 1 to 3 years after roads were decommissioned. Considering that the regeneration trajectory of the vegetation is likely to change in the future, we can expect temporal variations in the influence of different treatments for large mammal space use. Moreover, monitoring forest roads under a before-after control-impact design would have allowed us to assess the benefits of road decommissioning treatments compared to *status quo*. We thus cannot conclude about the medium– to long–term efficacy of road decommissioning treatments to restore boreal caribou habitat, and argue that further studies are needed. However, and despite the fact that restoration applications in the context of caribou conservation are relatively recent (e.g. Keim et al., 2019; Tattersall et al., 2020; Dickie et al., 2021), current management practices now aim at identifying the best methods to thwart several decades of habitat deterioration in the shortest amount of time possible.

Also, the poor fit of some of our statistical models indicates that some important covariates explaining variations in the use of decommissioned forest roads by large mammals were not measured in this study. Factors such as linear feature characteristics (e.g., width, vegetation height; Dickie et al., 2017a, b; Tigner et al., 2014), resource availability (e.g., Switalski and Nelson, 2011) or the size of adjacent land cover types (e.g., Lesmerises et al., 2013) could be considered in future studies.

Conservation implications

Forest roads that were closed, decompacted and planted with spruce trees were used most (or, maybe more appropriately, avoided less) by caribou compared to other treatments. This treatment granted the highest frequency of use by caribou, and was also identified by Lacerte et al. (2021) as the treatment most likely to lead to a mature coniferous forest typical of boreal caribou habitat. Decommissioning forest roads using the planted treatment in a landscape composed mostly of mature coniferous stands should improve landscape connectivity for caribou, i.e., by increasing the availability of suitable patches among which caribou can travel (Bauduin et al., 2018). Moreover, creating larger, continuous patches of conifer forest may allow caribou to efficiently space away from wolves (Lesmerises et al., 2013). Based on our results, we recommend that, when possible, forest roads surrounded by recent clearcuts or wetlands should be decommissioned using the planted treatment, as these roads were associated with an increased level of use by predators and were thus likely linked to a higher predation risk for caribou (see also DeMars and Boutin, 2018; St-Pierre et al., 2021, submitted).

Although we highlighted the short-term efficacy of incremental restoration efforts when decommissioning forest roads, caribou recovery efforts cannot rely solely on road network management, especially considering the myriad of other factors influencing space-use patterns of large mammals (see also Tattersall et al., 2020; Dickie et al., 2021) and the time needed for habitat to recover. Consequently, we argue that the decommissioning of forest roads should be accompanied by other conservation strategies, starting first and foremost with broad-scale habitat protection planning (e.g., Ray, 2014), and, where needed, more hands-on strategies such as alternate prey and predator control, maternal penning, and translocations (Johnson et al., 2019; Serrouya et al., 2019). Only by protecting and restoring large swaths of boreal caribou habitat will we be able to curb the precipitous decline of this species at risk across its whole distribution in Canada. More broadly, our study suggests that active restoration may represent an efficient way to mitigate the negative impacts of road networks on wildlife, which are long-lasting and ubiquitous (Trombulak and Frissell, 2000; Benítez-López et al., 2010).

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SUPPORTING INFORMATION

Appendix 2.1: Principal coordinates of neighbour matrices (PCNM) best describing the spatial structure of the landscape (i.e., significantly related to the spatial structure of the frequency of use of the species, *P*-values ≤ 0.05), for boreal caribou, black bear, and moose.

PCNMs	**Boreal caribou**	**Black bear**	**Moose**
PCNM2	–	–	0.001
PCNM3	<0.001	–	<0.001
PCNM4	–	–	0.022
PCNM5	<0.001	–	–
PCNM9	0.040	0.008	–
PCNM12	–	–	0.004
PCNM13	–	–	–
PCNM16	–	0.023	–
PCNM17	0.002	–	–
PCNM18	0.011	0.006	–
PCNM19	0.029	–	–
PCNM25	0.004	–	–
PCNM29	0.001	0.032	–
PCNM31	0.002	–	–
PCNM36	–	0.005	–
PCNM43	–	–	0.040
PCNM48	–	–	0.007
PCNM56	0.049	–	
PCNM57	0.026	–	0.044

Appendix 2.2: ΔAIC_c (i.e., difference between the model and the most parsimonious model) of candidate models used to determine the best radius buffer to explain the use of decommissioned forest roads by boreal caribou, black bear, and moose for both undisturbed and disturbed land cover groups. Models assessed either the occurrence (logistic regression) or the frequency of use (binomial negative) of roads by the three species. Retained models are indicated in bold. The undisturbed and disturbed land cover types are described in Appendix 2.3.

Radius buffer	**Boreal caribou**		**Black bear**		**Moose**	
	Occurrence	**Frequency**	**Occurrence**	**Frequency**	**Occurrence**	**Frequency**
Undisturbed						
250 m	9.97	8.29	1.06	**0.00**	–	**0.00**
500 m	3.49	9.23	**0.00**	2.34	**0.00**	0.22
1 km	**0.00**	**0.00**	1.30	3.67	–	1.26
Disturbed						
250 m	17.84	6.39	**0.00**	2.94	**0.00**	**0.00**
500 m	15.34	**0.00**	0.30	0.57	10.40	0.38
1 km	**0.00**	–	–	**0.00**	–	0.45

Appendix 2.3: Mean ($\bar{X}$), standard deviation (SD), range (min–max), and description of land cover types (within 250-m, 500-m, and 1 km radius buffer surrounding road segments) used in the occurrence (logistic regression) and frequency of use (binomial negative) candidate models explaining use of roads by boreal caribou, black bear, and moose.

Variables	**Radius**	**$\bar{X}$ ± SD**	**Range**	**Model**		**Description**
				Occurrence	**Frequency**	
Wetlands	250-m	0.40 ± 1.30	0–9.25	–	Bear, moose	Bogs, fens, swamp, and sphagnum coniferous forests (%)
	500-m	0.69 ± 1.44	0–8.73	Bear, moose	–	
	1-km	0.71 ± 1.03	0–4.16	Caribou	Caribou	
Deciduous forests	250-m	1.14 ± 4.43	0–33.24	–	Bear, moose	Deciduous stands of all age classes (%)
	500-m	1.17 ± 3.35	0–17.39	Bear, moose	–	
Coniferous forests	1-km	21.01 ± 8.29	5.81–43.52	Caribou	Caribou	Coniferous stands >20 years old (%)
Natural disturbances	250-m	11.95 ± 13.60	0–55.71	Bear, moose	Moose	Fires, windthrows, and insect epidemics (%)
	500-m	16.12 ± 12.72	0–43.11	–	Caribou	
	1-km	17.68 ± 10.78	0.87–47.20	Caribou	Bear	
Recent clearcuts	250-m	57.99 ± 20.62	7.52–99.95	Bear, moose	Moose	Clearcuts ≤ 20 years old (%)
	500-m	46.58 ± 15.98	8.17–89.42	–	Caribou	
	1-km	39.11 ± 13.44	16.32–69.72	Caribou	Bear	
Road density	250-m	3.35 ± 1.04	1.40–6.50	Bear, moose	Moose	Density of forest roads (km/km^2)
	500-m	2.36 ± 0.75	0.80–4.25	–	Caribou	
	1-km	1.86 ± 0.54	0.75–3.01	Caribou	Bear	

For bear models, we included the intensity of use and local densities of their prey, namely caribou and moose. Conversely, we included predators of caribou and moose in their models; we included the intensity of use of wolves and bears, and the local densities of bears (we were unable to generate local densities of wolves because no wolf was ever captured on a forest camera). We also included the intensity of use and local density of moose in caribou models because of their influence on their shared predator, the wolf. We included the proportion of mature coniferous forests into caribou models, deciduous stands in bear and moose models, and wetlands in caribou and moose models, as these stands are generally selected by these respective species (Courbin et al., 2009; Peters et al., 2013; Ray, 2014). We also included the proportion of wetlands in bear models, as this predator was shown to use linear features more extensively in areas surrounded by peatlands (DeMars and Boutin, 2018; Mumma et al., 2019). We included natural disturbances, recent clearcuts and road density in all models, because disturbed areas are generally avoided by caribou (Courbin et al., 2009) and selected by bears and moose (Brodeur et al., 2008; Courbin et al., 2009; Peters et al., 2013; Mumma et al., 2021). We dropped the road use by wolves from caribou models, and the local density of moose from the moose occurrence model because of convergence issues.

Appendix 2.4: Mean and CI 95% ([Lower: Upper]) of the intensity of use (no. events per 100 cameras-days) of roads that were closed (n=46), decompacted (n=76), planted (n=74), or enriched (n=76), and of the surrounding environment (local density; n=141) by boreal caribou, gray wolf, black bear, and moose.

Treatments	**Boreal caribou**		**Gray wolf**		**Black bear**		**Moose**	
Closed	0.20	[0.11: 0.33]	0.11	[0.05: 0.21]	0.40	[0.26: 0.56]	3.74	[3.30: 4.22]
Decompacted	0.52	[0.38: 0.70]	0.06	[0.02: 0.13]	0.72	[0.55: 0.93]	2.73	[2.38: 3.11]
Planted	0.76	[0.58: 0.98]	0.06	[0.02: 0.14]	0.59	[0.43: 0.79]	2.05	[1.74: 2.40]
Enriched	0.23	[0.14: 0.35]	0.00		0.25	[0.15: 0.37]	2.98	[2.61: 3.38]
Local density	0.34	[0.26: 0.45]	0.00		0.04	[0.02: 0.09]	0.79	[0.65: 0.94]

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CONCLUSION GÉNÉRALE

RETOUR SUR LE CONTEXTE DE L'ÉTUDE

Les structures linéaires sont reconnues pour altérer l'intégrité biotique des écosystèmes naturels (Trombulak & Frissell 2000). Ainsi, leur démantèlement, à des fins de restauration d'un habitat forestier, semble être une approche prometteuse pouvant contribuer au rétablissement ou à la conservation des espèces menacées par ces perturbations (Johnson et al. 2019; Serrouya et al. 2020) telles que les populations boréales de caribous des bois (*Rangifer tarandus caribou*; LC 2002 c29; COSEPAC 2014, 2016). Les structures linéaires contribuent au déclin des populations de caribous en favorisant le déplacement de ses prédateurs, tels que le loup gris (*Canis lupus*) et l'ours noir (*Ursus americanus*; Tigner et al. 2014; Finnegan et al. 2018a; Dickie et al. 2017a, b, 2020), en plus d'augmenter la disponibilité des ressources alimentaires végétales pour l'ours et l'orignal (*Alces americanus*; Mosnier et al. 2008; Bastille-Rousseau et al. 2011; Laurian et al. 2012). Le démantèlement des structures linéaires a donc le potentiel de permettre une régénération végétale qui devrait ultimement mener à la restauration d'un habitat favorable au caribou, en contraignant les déplacements et en diminuant l'abondance des ressources alimentaires des prédateurs et des proies alternatives.

Les lignes sismiques et les chemins forestiers, qui représentent une proportion importante de l'ensemble des structures linéaires d'origine anthropique présentes au Canada, s'avèrent considérablement différentes tant au niveau fonctionnel que structurel (Desautels et al. 2009; Government of the Northwest Territories 2015; Dabros et al. 2018). De telles différences sont susceptibles d'influencer de manière contrastée les réponses floristiques et fauniques et, par conséquent, les approches nécessaires pour démanteler ces structures et y restaurer les habitats forestiers fonctionnellement représentatifs d'habitats non perturbés

(Dickie et al. 2017a; Filicetti et al. 2019; Finnegan et al. 2019). Cependant, la majorité des études réalisées au Canada portant sur la restauration active des structures linéaires ont été réalisées sur les lignes sismiques de l'Ouest canadien (p. ex. Filicetti et al. 2019; Dickie et al. 2021). Un manque considérable de connaissances subsistait quant aux effets du démantèlement des chemins forestiers sur la faune et la flore canadiennes, bien que ceux-ci constituent la perturbation linéaire la plus fréquente dans l'est du pays (Pasher et al. 2013). Ainsi, l'objectif principal de mon étude était d'évaluer l'effet du démantèlement des chemins forestiers sur l'établissement de la végétation ainsi que sur la réponse d'une communauté de grands mammifères. Pour ce faire, différents traitements de restauration active ont été évalués, suivant un gradient d'intensité de restauration : (1) fermés; (2) fermés et décompactés; (3) fermés, décompactés et plantés; (4) fermés, décompactés, plantés et enrichis.

RETOUR SUR LES PRINCIPAUX RÉSULTATS

EFFET DU DÉMANTÈLEMENT DES CHEMINS SUR L'ÉTABLISSEMENT DE LA VÉGÉTATION

L'objectif du premier chapitre était d'évaluer l'établissement de la végétation sur des chemins forestiers fermés depuis 3 à 4 ans, en fonction de quatre traitements visant à restaurer l'habitat du caribou boréal. La variation dans la composition et la structure de la végétation qui s'était établie dans les chemins forestiers traités était expliquée à 25 % par les types de traitements ainsi qu'à 5 % par l'environnement présent autour des chemins traités et par la largeur de l'assise du chemin (voir chapitre 1). J'ai montré que le démantèlement des chemins forestiers, particulièrement la décompaction, était une méthode efficace pour favoriser la reprise végétale dans l'assise du chemin, sans égard pour les espèces composant la régénération (comparativement à la fermeture employée seule). J'ai également montré que la plantation résultait en une revégétalisation susceptible de mener vers une pessière noire mature, l'habitat préférentiel du caribou. À l'inverse, les traitements fermés et décompactés favorisaient des essences végétales recherchées par les ours et les orignaux (c.-à-d. herbacées, arbustes fruitiers et arbres feuillus). Les traitements incluant l'enrichissement diminuaient l'abondance de ces espèces végétales au profit des épinettes noires, mais favorisaient légèrement les essences herbacées, et étaient donc moins souhaitables que le traitement fermé, décompacté et planté pour restaurer l'habitat du caribou boréal, en plus d'être plus coûteux.

RÉPONSE DES GRANDS MAMMIFÈRES AU DÉMANTÈLEMENT DES CHEMINS FORESTIERS

L'objectif de mon deuxième chapitre était d'évaluer l'utilisation des chemins traités faite par le caribou, le loup, l'ours et l'orignal. Mes résultats suggèrent que les caribous utilisaient davantage les chemins fermés, décompactés et plantés, comparativement aux chemins qui n'étaient que fermés à la circulation. En revanche, les données récoltées ne m'ont pas permis de mettre en évidence un effet des traitements sur l'utilisation des chemins faite par le loup, l'ours et l'orignal (seules des tendances ont été observées pour l'ours et l'orignal). De plus, le faible nombre de photos de loups ne nous a pas permis d'évaluer l'utilisation des chemins faites par les loups. Cependant, l'utilisation des chemins par les caribous, ours et les orignaux était influencée non seulement par l'intensité d'utilisation des autres mammifères, mais également par l'environnement entourant les chemins forestiers. Les ours utilisaient davantage les segments de route également utilisés par le caribou. Les caribous étaient, quant à eux, observés dans des chemins moins utilisés par les orignaux, mais plus utilisés par les ours. J'ai également constaté que les chemins adjacents à une plus forte proportion de forêts résineuses ou de milieux humides étaient plus utilisés par les caribous. Les chemins avoisinants une proportion élevée de perturbations naturelles ou de coupes forestières de moins de 20 ans étaient plus utilisés par les orignaux, alors que les chemins adjacents à des milieux humides étaient plus utilisés par les ours.

IMPLICATIONS DE L’ÉTUDE

IMPLICATIONS THÉORIQUES

La restauration de l’habitat est majoritairement réalisée dans l’optique de permettre le retour de la composition en espèces, de la structure ou des processus écologiques (p. ex. cycle des nutriments, succession végétale) d’un habitat perturbé (Stanturf et al. 2014). Notre étude a évalué l’efficacité d’une restauration de type réhabilitation (restauration fonctionnelle), qui consiste à restaurer la composition des espèces, la structure ou les processus écologiques d’un écosystème perturbé (Stanturf et al. 2014). Nos résultats ont montré que le démantèlement des chemins forestiers permettait une régénération végétale susceptible de mener à l’habitat potentiel pré-perturbation, ce qui pourrait contribuer à augmenter la naturalité du paysage (c.-à-d. l’état naturel des peuplements; *sensu* Barrette et al. 2020) et la résilience des peuplements (c.-à-d. l’intensité de perturbations qu’un écosystème peut subir sans modifier sa structure ou ses processus; *sensu* Gunderson 2000). En effet, Barrette et al. (2020) ont montré que la naturalité des peuplements diminuait avec l’intensification des aménagements forestiers, ces derniers générant des peuplements semi-naturels, altérés ou artificiels. De plus, les aménagements forestiers successifs risquent de nuire à la résilience des peuplements (Barrette et al. 2019) en générant des états alternatifs stables au lieu de stades de succession forestière naturels (Mori et al. 2017). Ces états alternatifs non désirés peuvent persister des siècles, voire des millénaires (p. ex. Jasinski & Payette 2005; Fletcher et al. 2014; Boulangeat et al. 2018), fixant la communauté végétale dans un état non-représentatif de l’écosystème présent avant la perturbation, ou des habitats adjacents. La résilience est fonction, entre autres, de la capacité de régénération des plantes présentes et donc de la proportion de peuplements naturels conservés près des perturbations (van de Leemput et al. 2018). Ainsi, la régénération est plus lente dans un territoire exploité par l’industrie forestière en raison de la faible proportion de peuplements non perturbés dans le paysage (van de Leemput et al. 2018). De surcroît, les routes forestières ont des conditions peu propices à la régénération (p. ex. compaction du sol élevée; St-Pierre et al. 2021). Sur des chemins forestiers, St-Pierre et al. (2021) ont montré que la restauration passive résultait parfois en une végétation représentative d’un état alternatif. En effet, certains chemins étaient régénérés en essences arbustives (p. ex. aulnes *Alnus* spp.) au lieu d’arbres résineux. Ainsi, nos résultats ont montré que, même dans un secteur perturbé par la récolte forestière, la restauration active permettait d’éviter la dénaturalisation et d’augmenter la résilience du paysage en orientant la trajectoire de régénération de la végétation vers la structure et la composition représentative de la pessière mature d’origine. Ces résultats novateurs sont importants et pertinents dans le domaine de la restauration des écosystèmes naturels.

IMPLICATIONS POUR LA CONSERVATION DES POPULATIONS BORÉALES DE CARIBOU DES BOIS

Les structures linéaires, dont notamment les chemins forestiers, sont considérées depuis longtemps comme nuisibles aux populations de caribou boréaux (p. ex. Dyer et al. 2001; Leblond et al. 2011; Rudolph et al. 2017). Leur démantèlement a été suggéré afin de diminuer la pression de prédation sur le caribou en réduisant les déplacements des prédateurs, mais également dans le but de restaurer un habitat favorable au caribou (Johnson et al. 2019; Serrouya et al. 2020). Mon projet constitue une des premières études réalisées dans l’est du Canada à s’intéresser à l’efficacité de la fermeture et du démantèlement des chemins forestiers pour la restauration de l’habitat du caribou boréal (mais voir SÉPAQ 2014 qui ont effectué une simple fermeture d’accès). Mes résultats sont également novateurs par la comparaison de traitements suivant un gradient d’intensité des efforts de restauration. En effet, les études touchant au démantèlement des lignes sismiques se sont souvent intéressées à une seule méthode ou combinaison de traitements pour évaluer l’efficacité de la restauration de l’habitat du caribou (p. ex. Keim et al. 2019; Dickie et al. 2021). À ce jour, l’évaluation du niveau d’efforts de restauration nécessaire pour réaliser un démantèlement efficace pour la restauration de l’habitat du caribou boréal n’avait pas été faite. Mon étude contribuera ainsi à définir les traitements à inclure ou à exclure des futurs projets de démantèlement des chemins forestiers. La combinaison de la fermeture, de la décompaction et de la plantation était le traitement le plus efficace pour restaurer l’habitat du caribou boréal. À l’inverse, malgré l’objectif de faciliter la revégétalisation naturelle (p. ex. Filicetti et al. 2019), la décompaction appliquée seule favorisait les espèces végétales prisées par l’ours et l’orignal (c.-à-d. les herbacées, les arbustes fruitiers et les arbres feuillus; chapitre 1). Également, mes résultats suggèrent qu'au lieu de favoriser l'établissement des épinettes noires, l'enrichissement était bénéfique aux herbacées, des espèces recherchées par l'ours (Bastille-Rousseau et al. 2011; Switalski & Nelson 2011), démontrant ainsi l'inutilité d'investir des ressources additionnelles à enrichir les sols où la plantation doit être réalisée (à tout le moins dans les conditions rencontrées dans mon aire d'étude).

L'évaluation de l'effet des traitements de restauration, des conditions environnementales (c.-à-d. les caractéristiques des chemins et l'environnement adjacent) et de l'utilisation sympatrique des chemins par les mammifères sur l'établissement de la végétation ainsi que sur l'utilisation des chemins par les mammifères a permis de clarifier l'importance des facteurs pouvant influencer le succès du démantèlement. Ces résultats permettent également de moduler les efforts de restauration (Ray 2014). Dans les paysages fortement fragmentés ou pour des populations de caribous dont le déclin est principalement induit par une forte densité de prédateurs, le démantèlement pourrait être priorisé sur des segments de chemins adjacents à des milieux humides, des perturbations naturelles ou des coupes récentes, segments plus utilisés par l'ours et l'orignal (proie principale du loup), afin de réduire le risque de prédation (voir également DeMars & Boutin 2018; St-Pierre et al. en révision). Dans les secteurs où l'objectif de la restauration est la création d'un corridor de déplacement des populations de caribous, le démantèlement pourrait être effectué sur des segments de chemins adjacents à des peuplements résineux, segments plus utilisés par le caribou, afin d'augmenter la connectivité des habitats favorables (Lesmerises et al. 2013; Bauduin et al. 2018).

À l'échelle de la forêt boréale canadienne, l'aire de répartition du caribou boréal chevauche une grande diversité de conditions environnementales comportant divers types d'habitats naturels et de perturbations anthropiques (Environnement Canada 2011; Pasher et al. 2013). L'influence de l'environnement adjacent aux structures linéaires a également été mentionnée dans l'ouest du pays (p. ex. Finnegan et al. 2019; Tattersall et al. 2020), ce qui pourrait influencer l'efficacité de nos traitements s'ils étaient appliqués à l'échelle canadienne (et mondiale). Cependant, certains de nos résultats ont également été observés sur les lignes sismiques de l'ouest du pays dont, par exemple, la plus forte utilisation des lignes adjacentes à des milieux humides par l'ours noir (DeMars & Boutin 2018). De plus, les résultats de notre étude suggèrent que les types de traitement expliquaient davantage l'établissement de la végétation 3–4 ans après la restauration que les autres variables environnementales considérées. Ainsi, le traitement combinant la fermeture, la décompaction et la plantation aurait le potentiel de mener à une forêt résineuse mature favorable au caribou, mais défavorable aux prédateurs et proies alternatives dans des habitats similaires à ceux étudiés. Je soutiens ainsi que mon étude peut servir de point de départ à des projets de restauration situés dans un écosystème forestier différent de celui rencontré dans mon aire d'étude. Concrètement, mes résultats serviront à la conception d'un plan de restauration de l'habitat d'un corridor de déplacement favorable à une plus grande connectivité fonctionnelle entre les populations de Lac-des-Cœurs (notre aire d'étude) et de Pipmuacan, située plus au nord. Ce corridor sera créé et aménagé par le Conseil de la Première Nation des Innus Essipit, avec qui mon projet a été mené de concert.

LIMITES DE L'ÉTUDE

Mon étude a été réalisée seulement quelques années après les travaux de restauration, soit 3 à 4 ans pour l'établissement de la végétation (chapitre 1) et 1 à 3 ans pour l'utilisation des chemins par les mammifères (chapitre 2). Mes résultats se limitent donc à des différences d'efficacité des traitements à court terme. De plus, le faible nombre de photos de loups ne nous a pas permis d'évaluer l'utilisation des chemins faites par les loups. La trajectoire de régénération de la végétation est susceptible de changer au cours des prochaines années, ce qui risque également de modifier l'utilisation des chemins faite par les mammifères. Bien que les résultats de cette étude ne soient pas à même de statuer définitivement sur l'efficacité des traitements à restaurer un habitat forestier mature à terme, ils nous renseignent sur la trajectoire de régénération à court terme, et soulignent que le démantèlement a le potentiel de contribuer à restaurer un habitat favorable au caribou. Un suivi à long terme de l'établissement de la végétation et de l'utilisation des chemins par les mammifères m'apparaît donc nécessaire afin de statuer sur l'efficacité des traitements de restauration utilisés dans mon étude.

Les traitements représentaient le groupe de variables le plus important pour expliquer la variation dans la distribution de la végétation. Toutefois, 71 % de la variation totale est demeurée inexpliquée (voir chapitre 1). Également l'ajustement de certains modèles (c.-à-d. l'aire sous la courbe et le R^2; voir chapitre 2) expliquant la variation de l'utilisation des chemins par les mammifères était faible, suggérant que d'autres facteurs potentiellement influents n'ont pas été pris en considération dans nos analyses. Ainsi, afin de mieux comprendre la composition et la structure des assemblages végétaux établis dans les chemins forestiers, des variables à fine (p. ex. conditions du sol; Tremblay et al. 2013; Finnegan et al. 2019) et large (p. ex. dispersion naturelle des espèces; Hart & Chen 2008; Kremer et al. 2012; Pinno & Hawkes 2015) échelles spatiales auraient pu être intégrées à l'étude.

Il est reconnu que la végétation présente dans les assises des structures linéaires peut avoir une influence importante sur les patrons d'utilisation et de déplacements du loup (p. ex. Dickie et al. 2017b; Finnegan et al. 2018a) ainsi que sur la disponibilité en nourriture pour l'ours et l'orignal (Bastille-Rousseau et al. 2011; Laurian et al. 2012). Toutefois, en raison de contraintes logistiques lors du déploiement du plan d'échantillonnage, les parcelles de végétation utilisées dans le premier chapitre de cette étude n'étaient pas toujours centrées sur les cônes de détection des caméras automatisées utilisées dans le deuxième chapitre. J'ai donc été contrainte de considérer l'effet de la végétation dans nos modèles statistiques du chapitre 2 à l'échelle du segment entier et non du tronçon de chemin faisant face à la caméra. La forte variation d'abondance des différentes espèces végétales entre les parcelles d'un même segment de chemin m'a par contre obligée à intégrer les valeurs d'abondance de la végétation à une échelle plutôt grossière. J'ai tenté d'inclure ces effets aux analyses du chapitre 2 en intégrant les valeurs propres de la pCCA réalisée au chapitre 1 pour étudier la variabilité de composition et de structure des assemblages végétaux en fonction des traitements et de différentes variables environnementales. Toutefois, inclure les traitements et les valeurs de la pCCA dans un même modèle résultait à inclure deux variables qui expliquent sensiblement la même variation puisque les traitements expliquaient 25 % des patrons de distribution des espèces végétales dans les tronçons de chemin étudiés. Les travaux de terrain ayant été en partie exécutés en amont de mon arrivée à la maîtrise, il m’a été impossible de modifier le plan d’échantillonnage pour pallier à cet enjeu logistique.

J’ai évalué la variation de l’utilisation des chemins par les caribous, les ours et les orignaux à l’aide de caméras automatisées (voir chapitre 2). Gagnon-Labrosse et al. (en préparation) ont montré que le taux de détection des caméras pouvait varier entre les modèles de caméras utilisés. Selon des tests exécutés entre divers modèles de caméras à l’aide de passages contrôlés de chèvres Boer (*Capra aegagrus hircus*), le modèle Stealth QS18V2 s’est avéré avoir le plus faible taux de détection (Gagnon-Labrosse et al. en préparation). Les caméras utilisées dans mon étude étaient des Stealth PX12FX, un modèle différent quoique produit par la même compagnie. Cette faible détectabilité pourrait en partie expliquer le peu d’observations de loups dans mon étude (chapitre 2). Keim et al. (2019) ont évalué que le taux de faux négatifs sur les lignes sismiques était de seulement 1,6 %, mais avec un modèle de caméras différent de celui utilisé dans mon projet. La présence de faux négatifs pourrait biaiser les résultats obtenus. Le taux de faux négatifs n’a cependant pas pu être calculé, car aucun site ne comptait deux caméras ou plus, ce qui aurait permis de déterminer le pourcentage de passages manqués par l’une ou l’autre des caméras. Je suis donc d’avis que nos résultats représentent une image conservatrice de l’utilisation des chemins par les grands mammifères, puisque certains passages auraient pu être manqués par les caméras.

PERSPECTIVES

En conclusion, mon étude a permis d’évaluer l’efficacité du démantèlement des chemins forestiers pour la restauration de l’habitat du caribou en plus de définir les efforts de restauration nécessaires au succès du démantèlement. La combinaison de la fermeture, de la décompaction et de la plantation était la combinaison de traitements qui était la plus efficace pour la restauration de l'habitat du caribou, à tout le moins quelques années après le démantèlement. Évidemment, l'évaluation à long terme de l'efficacité de ces traitements devrait constituer l'objectif d'études futures. Des mesures transitoires (p. ex. éducation de peuplement) pourraient être nécessaires afin de s'assurer que la trajectoire de régénération végétale se dirige vers une pessière mature. Également, d'éventuels projets devraient évaluer davantage les déterminants influençant la reprise végétale dans les traitements. Ces connaissances nous permettraient de mieux comprendre l'établissement des espèces et ainsi de mieux prédire la régénération végétale avant même d'appliquer les traitements de fermeture et de démantèlement des chemins forestiers. Les traitements étudiés dans mon projet ont seulement influencé l'utilisation des chemins par le caribou, ce qui signifie que les traitements ne semblaient pas affecter l'utilisation par les prédateurs et proies alternatives à court terme. En ce sens, dans les prochaines études évaluant l'efficacité des pratiques de restauration active, des traitements de démantèlement comportant l'ajout d'obstacles aux mouvements tels que des débris ligneux (voir Keim et al. 2019; Dickie et al. 2021) pourraient être testés en combinaison avec la fermeture, la décompaction et la plantation.

La restauration de l'habitat par le démantèlement des chemins forestiers n'est pas seulement importante pour la conservation du caribou boréal au Canada, mais également pour toutes les sous-espèces de caribous et de rennes à l'échelle mondiale ainsi que toutes les espèces animales et végétales se trouvant affectées par la perte, l'altération et la fragmentation des forêts matures résineuses. Par exemple, plusieurs espèces de vertébrés sélectionnent les pessières matures en forêt boréale et souffrent également des pratiques forestières intensives (p. ex. campagnol à dos roux de Gapper *Myodes gapperi*, grimpereau brun *Certhia americana*, sittelle à poitrine rousse *Siita canadensis*, martre d'Amérique *Martes americana*; Drapeau et al. 2003; St-Laurent et al. 2008; Cushman et al. 2011; Fauteux et al. 2012). De telles espèces pourraient donc être favorisées par la restauration de l'habitat du caribou boréal. En effet, le caribou est parfois considéré comme espèce parapluie, c'est-à-dire que la préservation de l'habitat du caribou préserve également l'habitat d'autres espèces (Bichet et al. 2016; Drever et al. 2019). Ainsi, la restauration de l'habitat par le démantèlement des chemins forestiers est une méthode pertinente à instaurer pour la conservation des espèces en péril, mais également pour toutes les espèces affectées par la perte d'habitat liée à l'augmentation de la densité des perturbations anthropiques linéaires à travers le monde (Foley et al. 2005; Maxwell et al. 2016; WWF 2020).

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