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RÉGÉNÉRATION DES CHEMINS FORESTIERS ET UTILISATION PAR LES GRANDS MAMMIFÈRES DANS UN CONTEXTE DE CONSERVATION DU CARIBOU FORESTIER

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PAR

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RÉSUMÉ

Les perturbations anthropiques linéaires — dont les chemins forestiers — ont d'importants effets négatifs sur le caribou forestier (*Rangifer tarandus caribou*), une espèce menacée au Canada. Comprendre comment ces perturbations se régénèrent et influencent le caribou suite à leur création et leur utilisation par l'industrie s'avère essentiel pour orienter les travaux de restauration de l'habitat du caribou. Notre premier objectif était de décrire les caractéristiques qui influencent la composition de la régénération naturelle des chemins forestiers et de déterminer les facteurs qui empêchent son établissement. Nos hypothèses voulaient que la composition de la régénération allait dépendre de facteurs opérants à petite, moyenne et grande échelles spatiales et que l'établissement de la régénération allait dépendre principalement de la compaction de l'assise du chemin. Nous avons testé ces hypothèses à l'aide d'inventaires de végétation réalisés dans 56 tronçons de chemins forestiers répartis dans trois aires d'études de la forêt boréale québécoise. Nos résultats ont permis de souligner le rôle important du milieu environnant et de la compaction de l'assise des chemins sur la régénération. Notre deuxième objectif était de déterminer le rôle des caractéristiques des chemins sur leur utilisation par les espèces de grands mammifères impliqués dans le processus de compétition apparente avec le caribou, soit le loup gris (*Canis lupus*), l'ours noir (*Ursus americanus*) et l'orignal (*Alces americanus*). Nos hypothèses voulaient que les chemins facilitant les déplacements du loup soient davantage utilisés par celui-ci, que ceux facilitant l'accès à de la nourriture soient plus utilisés par l'ours noir et l'orignal et que l'utilisation des chemins par le caribou soit somme toute faible. Nos analyses supportent ces hypothèses et soulignent le rôle des caractéristiques des chemins sur leur utilisation par les grands mammifères. Nos résultats offrent une première description de la régénération naturelle des chemins en forêt boréale et pourraient bénéficier à d'autres espèces également impactées par les structures anthropiques linéaires. Ce mémoire souligne la nécessité de démanteler activement les chemins en plus d'identifier certains critères permettant de mieux orienter les efforts de restauration des habitats fauniques en forêt boréale.

Mots clés : Caribou forestier, Restauration de l'habitat, Perturbation linéaire, Chemin forestier, Régénération, Forêt boréale, Perturbation anthropique

ABSTRACT

Linear anthropogenic features—including logging roads—have important negative effects on boreal populations of woodland caribou (*Rangifer tarandus caribou*), a threatened species in Canada. Understanding how these features naturally regenerate and may impact caribou after being built and used by forest industries is essential to orient the restoration of suitable caribou habitat. Our first objective was to describe the composition of natural regrowth on logging roads and to determine which drivers may compromise its establishment. Our hypotheses were that regrowth composition would be driven by covariates operating at fine, intermediate and broad spatial scales and that regrowth establishment would be mainly driven by soil compaction. We tested these hypotheses using vegetation survey data collected from 56 logging roads. Our results showed the role of both soil compaction and the surrounding environment on regrowth. Our second objective was to document how the characteristics of logging roads influence their use by large mammals involved in apparent competition with caribou, i.e. gray wolves (*Canis lupus*), black bears (*Ursus americanus*) and moose (*Alces americanus*). We hypothesized that wolves use of roads with characteristics that facilitate movement would be higher, while black bears and moose use would be higher on roads that increase access to forage. Our analyses provided support to our hypotheses and underline the role of road characteristics on their use by large mammals. Our results offer the first description of logging road regrowth patterns in the boreal forest and could benefit other species impacted by anthropogenic linear features. This thesis underlines the need to actively decommission logging roads and offers some criteria to guide restoration efforts of wildlife habitat in boreal forest.

Keywords: Boreal caribou, Habitat restoration, Linear feature, Logging road, Regrowth, Boreal forest, Anthropogenic disturbances

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

INTRODUCTION GÉNÉRALE

POPULATION MONDIALE, PERTURBATIONS ET BIODIVERSITÉ

La croissance rapide de la population mondiale génère de plus en plus de pression sur les écosystèmes à l’échelle du globe (Crutzen, 2002 ; Steffen et coll., 2011a, 2011 b). Cette croissance rapide génère différents phénomènes qui menacent l’intégrité des milieux naturels, au point où les taux d’extinction des espèces animales et végétales s’approchent désormais de ceux des extinctions de masse précédentes (Barnosky et coll., 2011, 2012) et s’accentueront dans le futur (Pim et coll., 2006, 2014 ; Andermann et coll., 2020). L’augmentation des perturbations anthropiques due à la croissance de la demande en ressources affecte directement les communautés animales et végétales (Franklin et coll., 2016 ; Newbold et coll., 2015), dégrade et fragmente les habitats (Ceballo et Erhlich, 2002 ; Tillman et coll., 2017), perturbe les services écosystémiques (Brandon, 2014 ; Pohjamies et coll., 2017 ; Sing et coll., 2017) et représente une des causes importantes de la perte de biodiversité mondiale (Purvis et coll., 2000 ; Hoffman et coll.,2010 ; Martinez-Ramos et coll., 2016). Les écosystèmes forestiers sont particulièrement touchés par les perturbations anthropiques en raison de leur utilisation pour l’extraction de ressources ligneuses, gazières ou pétrolières (entre autres) et de leur conversion en terres agricoles (Hosonuma et coll., 2012 ; Potapov et coll., 2017). De 2000 à 2012, il a par exemple été estimé que la perte du couvert forestier en forêt tropicale s’est accentuée à un rythme de 2101 km²/année (Hansen et coll., 2013). Ces perturbations sont responsables d’une augmentation du risque d’extinction pour plusieurs espèces animales (Barlow et coll., 2016 ; Tracewski et coll., 2016) et menacent directement la biodiversité, particulièrement lorsqu’elles touchent des forêts qui se situent dans des paysages auparavant intacts (Betts et coll., 2017).

PERTURBATIONS ANTHROPIQUES EN FORÊT BORÉALE

La forêt boréale représente environ 30 % des forêts mondiales et est l'un des plus importants biomes terrestres. Cet écosystème fait face à des pressions de plus en plus importantes associées à l'augmentation de la population et, conséquemment, à la demande en ressources (Gauthier et coll., 2015, Trumblore et coll., 2015, Franklin et coll., 2016). Au Canada, elle occupe plus de 270 millions d'hectares (Brandt et coll., 2013) et représente une source d'approvisionnement pour différents secteurs économiques, dont (principalement) plusieurs industries des domaines forestier, pétrolier, gazier, mais également minier et énergétique (Brandt et coll., 2013 ; Venier et coll., 2014 ; Dabros et coll., 2018 ; Ressources naturelles Canada, 2020). L'importance de l'empreinte spatiale de ces industries et des perturbations qui en découlent varie selon un gradient longitudinal ; le développement gazier et pétrolier est plus important en Alberta tandis que l'exploitation forestière génère la plus importante empreinte industrielle dans la forêt boréale de l'Ontario et du Québec (Pasher et coll., 2013).

Ces deux industries génèrent différents types, formes, étendues et intensité de perturbations. D'une part, l'extraction des ressources pétrolières nécessite le repérage de gisements à l'aide de relevés sismiques s'effectuant le long de corridors où toute la végétation est retirée pour faciliter le déplacement de la machinerie associée à ces tests (Gouvernement des Territoires du Nord-Ouest, 2012). Historiquement, les lignes d'exploration sismiques prenaient une forme linéaire d'une largeur variant de 5 à 10 m, mais depuis le milieu des années 1990, elles peuvent mesurer aussi peu que 1,5 m de largeur et être plus sinueuses afin de tenter d'en limiter les impacts sur la ressource ligneuse et les espèces fauniques (Dabros 2018). Néanmoins, le paysage boréal de l'ouest du pays est scarifié par plus d'un million de kilomètres de lignes d'exploration sismique (Timoney et Lee, 2001), avec des régions où les densités de ces structures peuvent atteindre 10 km/km² (Lee et Boutin, 2006). Aux lignes d'exploration sismique s'ajoutent les puits de forage, les pipelines et les chemins d'accès qui fragmentent d'autant plus la forêt boréale de l'ouest du pays (Brant et coll., 2013). L'exploitation forestière génère quant à elle d'imposants parterres de coupe que l'on retrouve à différents stades de régénération. À titre d'exemple, la superficie récoltée atteignait 7 590 km² en 2018 au Canada, dont 2020 km² au Québec uniquement, principalement en forêt boréale, pour tous les types de couverts forestiers confondus (Venier et coll., 2014 ; National Forestry Database, 2020). Aux parterres de coupe en régénération s'ajoutent les centaines de milliers de kilomètres de chemins forestiers nécessaires au transport de la matière ligneuse (Pasher et coll., 2013 ; Brandt et coll., 2013 ; Waga et coll., 2019).

Les impacts générés par ces deux industries sont tels qu'ils sont considérés comme des agents significatifs de la dynamique forestière boréale (Grondin et coll., 2014 ; Pickell et coll., 2014 ; Curtis et coll., 2018), ayant même poussé les paysages boréaux à l'extérieur de leur variabilité naturelle en ce qui attrait à la structure d'âge de leurs peuplements forestiers (Cyr 2009, Pickell et coll., 2015 ; Grondin et coll., 2018). Les perturbations anthropiques affectent plusieurs aspects de l'écosystème boréal dont les émissions de carbone (Kurz et coll., 2013), la biochimie des sols et des systèmes aquatiques (Kreutzweiser et coll., 2008a), l'hydrologie (Buttle et coll., 2005), la structure d'âge et la composition des peuplements (Bouchard et Pothier, 2011 ; Dabros et coll., 2017, 2018) en plus de fragmenter les paysages boréaux (Brandt et coll., 2013 ; Pattison et coll., 2016). Toutes ces modifications affectent ultimement les communautés animales ; plusieurs études dans les dernières années ont d'ailleurs documenté les effets des perturbations anthropiques sur certains taxons retrouvés en forêt boréale dont les arthropodes (Phillips et coll., 2006, Kreutzweiser et coll., 2008b), les amphibiens (Pearce et Venier, 2009), les oiseaux (Mahon et coll., 2019 ; Drapeau et coll., 2000, 2009 ; St-Laurent et coll., 2009), les mammifères (St-Laurent et coll., 2008 ; Fisher et Burton, 2018, Pattison et coll., 2020 ; Wittsche et coll., 2021) et, plus particulièrement, l'écotype boréal du caribou des bois (*Rangifer tarandus caribou*) (voir les références dans la section ci-dessous).

LE CAS DU CARIBOU DES BOIS (POPULATIONS BORÉALES)

L'écotype forestier du caribou des bois (aussi appelé « caribou boréal », ci-après caribou) est une des espèces emblématiques de la forêt boréale canadienne qui occupe une vaste superficie s'étendant de la Colombie-Britannique à Terre-Neuve-et-Labrador (Festa-Bianchet et coll., 2011). Les populations de caribous connaissent actuellement un déclin qui, depuis 2003, justifie le statut d'espèce menacée en vertu de la loi sur les espèces en péril du Canada (Loi sur les espèces en péril, 2002). Au Québec, la situation du caribou lui confère depuis 2005 le statut d'espèce vulnérable en vertu de la loi sur les espèces menacées ou vulnérables (Loi sur les espèces menacées ou vulnérables, 2005). Ce déclin s'explique principalement par une pression de prédation accrue qui est ultimement induite par l'augmentation de l'étendue des perturbations anthropiques dans son aire de répartition (Environnement Canada, 2011, 2012 ; Festa-Bianchet et coll., 2011 ; Johnson et coll., 2015 ; Johnson et coll., 2020). Historiquement, les populations de caribous ont su persister grâce à une stratégie de ségrégation spatiale vis-à-vis des autres cervidés comme l'orignal (*Alces americanus*) et le cerf de Virginie (*Odocoileus virginianus*), lui permettant de se séparer de son prédateur principal, le loup gris (*Canis lupus*), en sélectionnant les habitats peu productifs comme les tourbières et les pessières matures (Seip, 1992 ; James et coll., 2004). Ce faisant, le caribou pouvait limiter le taux de rencontre avec le loup ainsi que le risque de prédation. Toutefois, les diverses formes de développement anthropique dans l'habitat du caribou ont eu pour effet d'exacerber la prédation sur ce dernier, notamment via le principe de compétition apparente (Holt, 1977 ; DeCesare et coll., 2010). En effet, la conversion d'habitats favorables au caribou en de jeunes peuplements en régénération favorables aux espèces de proies alternatives (p. ex. orignal) a favorisé une augmentation numérique de ces proies qui sont plus productives que le caribou (James et coll., 2004 ; Latham et coll., 2011). Cette hausse de la biomasse des proies alternatives a, à son tour, induit une augmentation de la taille des populations de leur prédateur commun (principalement le loup, mais au sud du fleuve Saint-Laurent le coyote *Canis latrans* [Frenette et coll., 2020]), résultant en une prédation plus importante sur le caribou (Wittmer et coll., 2007 ; Johnson et coll., 2020). La régénération feuillue des perturbations s'est aussi avérée favorable à l'ours noir en raison de la présence de différentes plantes qu'il consomme (Mosnier et coll., 2008 ; Bastille-Rousseau et coll., 2011). Bien que l'ours noir se nourrisse principalement de ressources végétales (Raine et Kansas, 1990 ; Romain et coll., 2013 ; Lesmerises et coll., 2015), cet omnivore peut tout de même exercer une pression de prédation importante sur les faons du caribou (Pinard et coll., 2012 ; Leclerc et coll., 2014 ; Mahoney et coll., 2016 ; Mumma et coll., 2019a). Le caribou se retrouve ainsi coincé dans une mosaïque forestière où les prédateurs sont de plus en plus nombreux et où l'évitement du loup augmente les risques de prédation par l'ours noir (Leblond et coll., 2016) à un point tel que la prédation par l'ours noir peut s'avérer être le facteur principal limitant la croissance de certaines populations (p.ex. population de Charlevoix, Johnson et coll., 2019).

Les perturbations anthropiques linéaires, telles que les lignes d'exploration sismique, les chemins forestiers et les lignes de transport d'énergie (pipelines, réseau électrique), représentent un cas particulier ayant fait l'objet de plusieurs études dans les dernières années. Étant évitées par le caribou (James et Stuart-Smith, 2000 ; Leblond et coll., 2011 ; Dussault et coll., 2012 ; Mumma et coll., 2019b), ces structures ont des conséquences négatives sur plusieurs aspects de son écologie spatiale dont la taille de son domaine vital (Leblond et coll., 2013 ; Beauchesne et coll., 2014), les déplacements (Dyers et coll., 2002 ; Beauchesne et coll., 2013), sa sélection d'habitat (Dyers et coll., 2001 ; Leclerc et coll., 2012), sa fidélité au site (Faille et coll., 2010, Lafontaine et coll., 2017) et la quantité d'habitat fonctionnellement disponible (Leblond et coll., 2011, 2013 ; Johnson et coll., 2015). À l'inverse, les structures anthropiques linéaires sont sélectionnées par le loup (Latham et coll., 2011 ; Pigeon et coll., 2020, Dickie et coll., 2020, Malcolm et coll., 2020) en raison du déplacement facilité sur ces structures par rapport au milieu forestier (Dickie et coll., 2017 ; Kittle et coll., 2017 ; Muhly et coll., 2019). Par conséquent, il a été montré que le taux de rencontre entre le caribou et le loup augmentait à proximité des perturbations anthropiques linéaires (Whittington et coll., 2011 ; Mumma et coll., 2017 ; McKay et coll., 2021) résultant en un plus faible taux de survie du caribou dans ces secteurs (Leblond et coll., 2013 ; Mumma et coll., 2018). La sélection des structures linéaires par le loup est d'autant plus importante dans les tourbières (Mumma et coll., 2019), nuisant directement à la stratégie d'évitement spatial du caribou (DeMars et

Boutin, 2018). Ces structures peuvent aussi être favorables à l’ours noir (Tigner et coll., 2014 ; Dickie et coll., 2020) et aux proies alternatives (Beyer et coll., 2018 ; Mumma et coll., 2018) en raison de la régénération qu’on y trouve qui représente une source de nourriture potentielle (Finnegan et coll., 2018, 2019).

PERTURBATION TOTALE, AUTOSUFFISANCE ET DÉMANTÈLEMENT DES STRUCTURES LINÉAIRES

En raison du nombre grandissant d’études documentant l’effet des perturbations de l’habitat sur la survie et la persistance des populations de caribous, Environnement Canada a proposé en 2011 un modèle reliant le taux de perturbation total (naturel et anthropique) retrouvé dans l’aire de distribution d’une population de caribou, à sa probabilité de se maintenir dans le temps (Environnement Canada, 2011). Basé sur ce modèle, le niveau de perturbation dans l’aire de répartition d’une population ne devrait pas dépasser 35 % de la superficie pour qu’une population ait au mieux une probabilité d’autosuffisance de 60 % dans le temps. Cependant, plusieurs populations de caribou se retrouvent dans des secteurs où le niveau de perturbation dépasse largement ce seuil au-delà duquel basculerait la probabilité d’autosuffisance (p. ex. Chinchaga : 76%, Little Smoky : 87 %, Charlevoix : 80 %, Pipmuacan : 59 % ; Environnement Canada, 2011 ; Johnson et coll., 2020), soulignant l’importance de restaurer certaines composantes de l’habitat de ces populations. Plus précisément, le démantèlement actif des perturbations anthropiques linéaires a été ciblé comme prioritaire étant donné leur importante contribution au niveau de perturbation de l’habitat (Sorensen et coll., 2008 ; Rudolph et coll., 2017 ; Lacerte et coll., 2021) et de leurs effets négatifs sur le caribou (Hervieux et coll., 2013 ; Johnson et coll., 2019 ; McKay et coll., 2020). Cette mesure de conservation est cependant très coûteuse (Filicetti et coll., 2019 ; Johnson et coll., 2019) et ne peut être envisagée pour certaines voies d’accès prioritaires au territoire ; il s’avère donc impossible de démanteler en totalité les centaines de milliers de kilomètres de structures linéaires existantes au Canada. Par conséquent, caractériser les facteurs qui empêchent l’établissement de la régénération naturelle des perturbations linéaires et documenter quelles sont les caractéristiques qui influencent leur utilisation par les grands mammifères s'avèrent des étapes importantes d'acquisitions de connaissances scientifiques pour ultimement prioriser la remise en production des perturbations linéaires les plus problématiques pour la survie du caribou.

Jusqu'à présent, la majorité des études ayant comme sujet la régénération des perturbations linéaires et leur utilisation par les grands mammifères ont été réalisées dans le cas des lignes d'exploration sismique dans les régions de l'ouest du Canada, où ces structures représentent la principale forme de perturbation. Ces études ont montré qu'une part importante des lignes d'exploration sismique ne se régénère pas suite à leur utilisation par l'industrie (Lee et Boutin, 2006) et que celles construites dans des milieux humides présentaient généralement le plus faible potentiel de régénération (van Rensen et coll., 2015 ; Finnegan et coll., 2019). Ces lignes sismiques à la régénération éparse et avec une faible hauteur étaient davantage utilisées par le loup en raison des déplacements qui y sont plus faciles que dans la forêt adjacente (Dickie et coll., 2017, 2020). Dans les cas où la régénération s'installait, celle-ci était dominée par des essences herbacées et arbustives tolérantes aux perturbations qui diffèrent de celles retrouvées dans un stade de forêt non perturbée (Finnegan et coll.,2018a) et qui représentent une source de nourriture pour les proies alternatives et l'ours noir (Finnegan et coll., 2018a, 2019 ; Tattersall et coll., 2020).

Très peu d'études ont cependant abordé le cas des chemins forestiers. Cette sous-représentation dans la littérature est problématique, car bien que les lignes d'exploration sismique et les chemins forestiers soient tous les deux des perturbations anthropiques linéaires, ces structures diffèrent fondamentalement dans la façon dont elles sont construites, mais aussi par leur association avec d'autres types de perturbations. Tout comme pour les routes, la construction de lignes sismiques nécessite le déboisement et la compaction du sol (Dabros et coll., 2018). Cependant, plusieurs étapes additionnelles sont nécessaires dans le cas des chemins forestiers, dont des travaux d'excavation intensifs permettant d'assurer une structure solide, le retrait des débris organiques, l'assèchement de la surface, la mise en forme de fossés et, dans certains cas, l'ajout de matériaux granulaires (p. ex. gravier, sable ; Ordre des ingénieurs forestiers du Québec, 2009). Depuis les dernières années, une attention particulière est portée au maintien et à la protection des racines des arbustes et de la banque de graines dans le cas des lignes sismiques afin de maximiser les probabilités de régénération naturelle (Gouvernement des Territoires du Nord-Ouest, 2012), une différence marquée qui contraste avec les méthodes de construction des chemins où l'étape du déboisement comprend le retrait des arbustes, des broussailles, du bois mort et des branches de l'emprise (Ordre des ingénieurs forestiers du Québec, 2009). Les chemins forestiers sont aussi construits de concert avec la coupe forestière afin d'accéder et d'extraire le bois des parterres de coupes (Ordre des ingénieurs forestiers du Québec, 2009). Ainsi, la régénération présente sur les chemins est potentiellement soumise à diverses formes d'altération des conditions de croissance associées aux coupes forestières telles qu'une exposition accrue à la lumière, une croissance accélérée des arbustes et de forts vents typiques des zones de bordure (Matlack, 1993 ; Chen Jiquan et coll., 1995, Mascuria-Lopez et coll., 2006 ; Boucher et coll., 2011). Finalement, les chemins forestiers peuvent être utilisés par d'autres usagers de la forêt (p.ex. pêcheurs, chasseurs, trappeurs, amateurs de plein air, propriétaires de chalet) longtemps après leur création en raison de l'accessibilité qu'ils offrent à des territoires qui étaient jusque-là relativement inaccessibles (Trombulak et Frissel, 2000 ; Brinkman et coll., 2007 ; Coffin, 2007 ; Daigle, 2010).

Considérant les différences dans leur construction, l'association des chemins forestiers avec d'autres formes de perturbation et leur utilisation par d'autres usagers que l'industrie, il apparaît important d'étudier spécifiquement le potentiel de régénération des chemins forestiers afin d'identifier les facteurs propres à ce type de structure qui en ralentissent la régénération et qui, conséquemment, influencent leur utilisation par le caribou, l'orignal, l'ours noir et le loup gris. La connaissance des facteurs qui facilitent ou contraignent la régénération végétale des assises des chemins et qui favorisent leur utilisation par le caribou, ses prédateurs et ses compétiteurs pourrait permettre de mieux cibler les chemins nécessitant des efforts de démantèlement actifs (Ray, 2014).

OBJECTIFS ET SOMMAIRE DES RÉSULTATS

L’objectif principal de ce mémoire était de caractériser la régénération arbustive et arborescente présente sur les chemins forestiers et d’identifier les facteurs qui influencent l’utilisation de ces chemins par le caribou, l’orignal, l’ours noir et le loup gris. Plus précisément, le premier objectif (chapitre 1) consistait à identifier les facteurs qui influencent la composition en essences de la régénération arbustive et arborescente retrouvée sur les chemins ou qui en empêchent l’établissement dans l’habitat du caribou. Le deuxième objectif (chapitre 2) visait à déterminer l’effet des caractéristiques des chemins sur leur utilisation par le caribou, l’orignal, l’ours noir et le loup gris.

Relativement au premier objectif, nous avons émis l’hypothèse que la composition en essences de la régénération allait être influencée à la fois par des facteurs à grande échelle comme la longitude, la latitude et le nombre de degrés-jours de croissance, par des variables à moyenne échelle comme le type de peuplement adjacent et finalement par des variables à petite échelle comme la compaction de l’assise et l’âge du chemin. Nous avons aussi émis l’hypothèse que l’établissement de la régénération serait principalement influencé par le niveau de compaction de l’assise des chemins. Pour le deuxième objectif, nous avons émis les hypothèses que les chemins ayant des caractéristiques favorisant les déplacements du loup allaient être sélectionnés par celui-ci, que l’ours noir et l’orignal allaient plutôt sélectionner les chemins dont les caractéristiques facilitent l’accès à la nourriture et, finalement, qu’en tentant d’éviter les prédateurs et les proies alternatives, le caribou allait utiliser de manière très faible les chemins davantage utilisés par les prédateurs et l’orignal.

Les résultats du premier chapitre ont montré que la composition en essences de la régénération des chemins forestiers variait principalement en fonction du nombre de degrés-jours de croissance, du type de peuplement à proximité et en fonction de l’âge et de la compaction du chemin. Dans certains cas, la régénération suivait une trajectoire alternative de succession vers des essences feuillues tolérantes aux perturbations plutôt que vers une régénération résineuse semblable à celle des milieux environnants non perturbés. La compaction du sol était la variable la plus importante empêchant l’établissement de la régénération, mais le type de peuplements environnant jouait aussi un rôle ; la présence de milieux humides autour d’un chemin en limitait la régénération alors que ceux entourés par une plus grande proportion de peuplements résineux avaient une régénération davantage composée d’essences résineuses.

Les résultats du deuxième chapitre ont montré quant à eux que la probabilité d’utilisation d’un chemin forestier par le loup était reliée aux conditions qui facilitent ses déplacements (faible densité du couvert latéral). Conformément à mon hypothèse, l’ours noir et l’orignal utilisaient davantage les chemins plus jeunes où la nourriture disponible sous forme de régénération feuillue était la plus abondante. Nous n’avons cependant pas pu tester nos hypothèses dans le cas du caribou en raison d’un nombre trop faible de photos récoltées pour cette espèce.

Les résultats de cette étude montrent que la régénération naturelle et, par conséquent, l’utilisation des chemins par les grands mammifères varient grandement en fonction des caractéristiques intrinsèques des chemins, mais aussi en fonction du contexte spatial dans lequel ils sont enclavés. Les résultats soulignent l’importance de considérer les caractéristiques individuelles et l’environnement adjacent de chacun des chemins afin de cibler ceux qui ne peuvent se régénérer naturellement au bénéfice du caribou, et qui par conséquent deviendront prioritaires pour des efforts de démantèlement actif. Sur cette base, nous considérons qu’une simple catégorisation basée, par exemple, sur l’âge ou la classe d’un chemin (telle que déterminée par le système de classification de la voirie forestière) n’est pas suffisante pour bien caractériser le niveau de régénération de la végétation sur l’assise des chemins forestiers abandonnés.

CHAPITRE 1

FACTEURS INFLUENÇANT LA RÉGÉNÉRATION DES CHEMINS FORESTIERS EN FORÊT BORÉALE : IMPLICATIONS POUR LA RESTAURATION DE L'HABITAT DU CARIBOU FORESTIER

1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Les perturbations anthropiques associées à l'augmentation de la population humaine génèrent de plus en plus d'impacts sur les communautés végétales et animales à l'échelle du globe. La forêt boréale de l'Amérique du Nord n'échappe pas à ce phénomène et les préoccupations sont croissantes quant à la persistance des perturbations anthropiques linéaires au Canada en raison de leurs effets négatifs sur la faune et, particulièrement, sur les espèces menacées comme le caribou forestier (*Rangifer tarandus caribou*). Bien que plusieurs études se soient récemment attardées à l'état et à la distribution de la régénération des lignes d'exploration sismiques dans l'ouest du pays, peu d'études ont tenté de caractériser la régénération végétale des chemins forestiers qui représentent la principale forme de perturbation anthropique linéaire dans l'est du Canada. En raison des différences structurelles entre les lignes d'exploration sismiques et les chemins forestiers, les résultats obtenus dans l'étude des lignes sismiques pourraient ne pas être applicables aux chemins forestiers. Le but de cette étude était donc de 1) déterminer l'influence de différentes caractéristiques des chemins sur la composition en essence de la régénération et 2) caractériser les facteurs environnementaux qui peuvent empêcher l'établissement de la régénération naturelle des chemins forestiers. Nous avons testé ces questions à l'aide de données récoltées sur 56 tronçons de chemins forestiers distribués dans trois régions de la forêt boréale québécoise. Nous avons utilisé une analyse canonique des correspondances afin de caractériser la composition en essence de la régénération et des modèles de régression mixte pour déterminer l'influence de différentes variables abiotiques et biotiques sur l'établissement de la régénération. Le nombre de degrés-jours de croissance et la proportion de forêt résineuse entourant le chemin expliquaient la majeure partie de la variation de la composition en essence de la régénération. La composition de la régénération variait le long du gradient suivant : le nombre de tiges d'aulne (*Alnus spp.*) était plus important dans les chemins recevant un plus grand nombre de degrés-jours de croissance et qui étaient entourés d'une plus faible proportion de forêts résineuses alors qu'un plus grand nombre de tiges d'essences résineuses composait la régénération des chemins où le nombre de degrés-jours de croissance était plus faible et qui était entouré d'une plus grande proportion de peuplements résineux. La compaction du sol était la principale variable qui empêchait l'établissement de la régénération. Une plus grande proportion de milieux humides entourant le chemin contribuait aussi à une faible régénération. Nos résultats soulignent la lenteur du processus de régénération naturelle des chemins forestiers et l'importance de la restauration active des chemins qui devrait inclure la plantation manuelle d'arbres dans le contexte de restauration de l'habitat du caribou forestier.

Mots-clés : Caribou forestier, Restauration de l'habitat, Perturbation linéaire, Chemin forestier, Régénération végétale

Ce premier article, intitulé « *Drivers of vegetation regrowth on logging roads in the boreal forest : implications for restoration of woodland caribou habitat* », a été corédigé par moi-même ainsi que par les professeurs Pierre Drapeau et Martin-Hugues St-Laurent. Il a été accepté pour publication dans sa version finale en 2020 par les éditeurs de la revue *Forest Ecology and Management*[1] et publié en 2021. En tant que premier auteur, ma contribution à ce travail couvrait l'essentiel de la recherche, le développement de la méthode, l'exécution des analyses et la rédaction de l'article. Les professeurs Martin-Hugues St-Laurent et Pierre Drapeau ont fourni l'idée originale, assuré le financement du projet en plus d'avoir révisé et commenté les analyses et le texte de l'article.

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[1] St-Pierre, F., Drapeau, P., St-Laurent, M.-H., 2021. Drivers of vegetation regrowth on logging roads in the boreal forest: Implications for restoration of woodland caribou habitat. *Forest Ecology and Management* 482, 1-11.

1.2 DRIVERS OF VEGETATION REGROWTH ON LOGGING ROADS IN THE BOREAL FOREST: IMPLICATIONS FOR RESTORATION OF WOODLAND CARIBOU HABITAT

ABSTRACT

The worldwide increase in anthropogenic disturbances imposed by the expansion of land use practices has important effects on vegetation dynamics and animal communities. The North American boreal forest is no exception to this global trend, and there are growing concerns regarding the persistence of linear anthropogenic features across Canada because of their negative impacts on wildlife and, particularly, on threatened species such as the boreal caribou (*Rangifer tarandus caribou*). While many recent studies have investigated the state and distribution of regeneration on seismic lines in the western part of the country, few studies have characterized the natural regrowth of logging roads, the main type of anthropogenic linear features found in eastern Canada. As seismic lines and logging roads are structurally different, results from seismic line studies may not be easily generalized to logging roads. In this study, we therefore 1) assessed the influence of different characteristics on vegetation regrowth composition and 2) determined which environmental drivers may compromise natural regrowth on logging roads. We tested these questions using data collected from 56 1-km long road segments distributed in three different regions across Québec's boreal forest (eastern Canada). We used a canonical correspondence analysis to characterize the species composition of vegetation regrowth on logging roads and used mixed regression models to assess the influence of different biotic and abiotic variables on regrowth establishment. The number of growing degree-days and the proportion of coniferous stands in the surroundings of a road segment explained most of the variation in species composition of the vegetation on roads. Regrowth composition on roads was distributed along a gradient shifting from a high number of alder (*Alnus spp.*) stems (in the region with a higher number of degree-days) and a smaller proportion of coniferous stands (surrounding the road segment) to a higher number of coniferous stems in regions experiencing fewer growing degree-days where road segments were surrounded by a greater proportion of coniferous stands. Soil compaction was the most important variable impeding the establishment of vegetation on logging roads. A greater proportion of wetlands surrounding the road segment also contributed to poor regrowth. Our results underline the slow rate of passive regeneration of logging roads and the importance of road surface decommissioning, which should include tree planting, in the context of woodland caribou habitat restoration.

Keywords: Boreal caribou, Habitat restoration, Linear feature, Logging road, Vegetation regrowth.

INTRODUCTION

In the last decades, the magnitude of land use changes has drastically increased worldwide (Foley et al., 2005; Franklin et al., 2016). Anthropogenic disturbances linked with the expansion of land use practices can have long-lasting effects on vegetation dynamics (Venier et al., 2014; Pickell et al., 2015; Trumblore et al., 2015) and, ultimately, on animal communities (Wittmer et al., 2007; Siira-Pietikäinen and Haimi, 2009; St-Laurent et al., 2009). It has recently been shown that these pervasive effects on vegetation successional processes and animal species community structure can surpass those associated with natural disturbances (Cyr et al., 2009; Drapeau et al., 2009) and recent climate change in northern forests (Franklin et al., 2016; Danneyrolles et al., 2019). The Canadian boreal forest is no exception to this trend, with an estimated polygonal anthropogenic disturbance footprint of 24 million ha, to which we can add more than a million kilometers of linear features as a result of resource extraction (Timoney and Lee, 2001; Pasher et al., 2013).

The boreal ecotype of woodland caribou (*Rangifer tarandus caribou*; hereafter caribou) is currently designated as Threatened under the Canadian Species at Risk Act (Species at Risk Act, 2002), mainly in response to an increasing encroachment of human-induced disturbances in its range (Vors and Boyce, 2009; Festa-Bianchet et al., 2011; COSEWIC, 2014). First, human-induced disturbances convert caribou habitat into early-seral stands suitable to alternative prey (e.g. moose *Alces americanus*, white-tailed deer *Odocoileus virginianus*), leading to an increase of their densities, which then support increases in grey wolf (*Canis lupus*) densities. This numerical response results in an increase predation pressure on caribou (i.e. apparent competition; Holt 1977; see also Wittmer et al., 2005, 2007; DeCesare et al. 2010). Vegetation regrowth of anthropogenic disturbances can also benefit opportunistic predators such as black bear (*Ursus americanus*), known to induce significant calf mortality in caribou (Leclerc et al., 2014). Second, timber harvesting, oil, gas and mining exploration and extraction also result in an increase in linear features (e.g. logging roads, seismic lines, pipelines and power lines), which are now more common throughout caribou range. These linear features are known to contribute to caribou decline primarily through an alteration of predator-prey relationships (Leblond et al., 2013; Dickie et al., 2017b, Mumma et al., 2018). Not only do linear features negatively affect caribou space use patterns (Beauchesne et al., 2013, 2014; Lafontaine et al., 2017), they are also selected by grey wolves and black bears to facilitate their movements and increase their travel speed, prey search efficiency and access to areas previously less accessible (i.e. functional response) (Tigner et al., 2014; Dickie et al., 2017b). This can lead to an increase in caribou-wolf encounter rates along linear features (Whittington et al., 2011; Mumma et al., 2017) and facilitates predator access to caribou spatial refugia (DeMars and Boutin, 2018), resulting in lower individual survival close to roads (Leblond et al., 2013) and seismic lines (Mumma et al., 2018). Because of their direct effects on caribou survival, further concerns have been raised regarding the persistence of anthropogenic linear features in caribou range in recent years (Dabros et al., 2018).

Different types of linear features exist across caribou range. While seismic lines—narrow corridors cleared to allow energy exploration—are a common type in western Canada, logging (forest) roads represent the main linear features found in Ontario and Québec (Pasher et al., 2013). Recent studies have assessed vegetation regrowth composition and distribution along seismic lines and how long these features require to fully regenerate or at least reach a vegetation structure (e.g. density, height) at which they stopped being attractive to predators and prey (e.g., Prove et al., 1990; Lee and Boutin, 2006; Ray, 2014; van Rensen et al., 2015; Dickie et al., 2017b; Finnegan et al., 2018a, 2018b, 2019). However, to our knowledge, no studies have specifically characterized the vegetation regrowth of logging roads built to support timber harvesting operations and found at various stages of dereliction in caribou ranges.

Seismic lines are structures usually ranging from 5–10 m in width, although recent low impact seismic lines can be as narrow as 2 m; their construction implies tree removal, soil levelling and compaction (GNWT, 2012; Dabros et al., 2018). Similarly, the building of logging roads also requires the clearing of wide right-of-ways as well as soil compaction and levelling to facilitate timber transport (Ordre des ingénieurs forestiers du Québec, 2009). However, road construction also necessitates additional steps such as intensive excavation, the removal of organic debris, the digging of ditches, backfilling, and in some instances, importation of gravel and sand (Ordre des ingénieurs forestiers du Québec, 2009). In addition, while seismic lines are cut directly through relatively intact forest stands, logging roads are built conjointly with timber harvesting operations (Ordre des ingénieurs forestiers du Québec, 2009) and are thus subject to cumulative edge effects associated with clearcuts, such has a higher light exposure and temperature, lower humidity, greater shrub growth and altered wind conditions (Matlack, 1993; Chen Jiquan et al., 1995). Lastly, logging roads often improve public forest accessibility for hunters, trappers, fishers and people practising other recreational activities following timber harvesting (Rempel et al., 1997; Trombulak and Frissell, 2000; Brinkman et al., 2007), and are also associated with increases in housing and other building establishment (Coffin, 2007; Daigle, 2010).

Studies on seismic lines showed very poor vegetation regrowth following exploration. In some cases, less than 10% of lines successfully regenerated a woody stem cover greater than 50% after 35 years (Lee and Boutin, 2006). Regenerating species can differ between regions and ecosites, with lines located in lowland ecosites generally having the poorest regrowth (Lee and Boutin, 2006; van Rensen et al., 2015; Finnegan et al., 2019). Regrowth type on seismic lines also differed from the forest interior and was dominated by disturbance-tolerant taxa ranging from forbs and graminoids to ligneous species such as *Betula, Alnus* and *Salix spp*. (Finnegan et al., 2018a). Anthropogenic use of seismic lines also influenced the type of regrowth (Finnegan et al., 2018a) or even impeded it (van Rensen et al., 2015) to a point where controlling human presence might be of primary importance for seismic line restoration (Pigeon et al., 2016; Hornseth et al., 2018). These results are important for caribou recovery in western Canada. Likewise, assessing which factors drive regrowth in the case of logging roads is of primary importance in regions where commercial timber harvesting is the main anthropogenic disturbance.

Considering that seismic lines and logging roads differ in their construction and spatial association with other disturbances (cutblocks), the knowledge provided from studies focusing on regeneration of seismic lines may not be easily transferable and generalized to logging roads. In order to orient restoration efforts, a better understanding of the composition and structure of natural regrowth on logging roads is essential, considering the growing number of documented impacts of logging roads on caribou (e.g. Leclerc et al. 2012; Beauchesne et al., 2013, 2014) and wolf (Lesmerises et al. 2012; Muhly et al. 2019; Malcolm et al. 2020) behaviour and, ultimately, on caribou demography (e.g. Leblond et al., 2013; Lafontaine et al., 2017; Rudolph et al. 2017).

Consequently, our first objective was to document the species composition of natural regrowth observed on logging roads with varying characteristics. We hypothesized that species composition would be driven by a complex assemblage of large-scale variables, such as longitude, latitude and the number of degree-days, local-scale adjacent stand type and road characteristics, mainly age and soil compaction. We thus predicted that older roads with a less compacted soil surrounded by a higher proportion of coniferous stands would have coniferous regrowth similar in composition to that of the pre-disturbance vegetation. Inversely, younger and more compacted roads located in young, disturbed landscapes would have regrowth dominated by stems of plant taxa tolerant to disturbances or would have no regrowth at all. We also aimed at determining which of the above-mentioned road characteristics could compromise or limit woody vegetation regrowth as a whole using two regrowth parameters: the percentage of lateral cover and the occurrence of a woody stem with a measurable diameter at breast height (i.e. height >1.30 m) at the center of the road. We hypothesized that lateral cover and the occurrence of a woody stem with a height >1.30 m at the center of the road will be mainly driven by soil compaction, when controlling for other landscape and growing condition variables. Accordingly, we predicted that more compacted roads would have a lower percentage of lateral cover, and that the occurrence probability of stems >1.30 m tall in the middle of such roads would be lower.

MATERIALS AND METHODS

Study area, road selection and sampling design

We conducted this research project in one study area divided into three regions located on the north shore of the St. Lawrence River in Québec (Canada) (Figure 1.1). The first region included the Laurentides Wildlife Reserve and parts of the Parc national de la Jacques-Cartier (Québec, Canada; 47.3-47.7 °N, 71.0-71.5 °W, 2120 km²; hereafter LWR), a provincial park located approximately 50 km north-east of Québec City. This region is part of the Charlevoix caribou population range. The second region encompassed the northern section of the Saguenay-Lac-St-Jean (49.7-50.3 °N,70.6-71.2 °W, 3900 km²; LSJ) and is occupied by the Piraube and Portneuf caribou population ranges, while the third covers the western part of the Côte-Nord and Manicouagan caribou population ranges (49.6-50.5 °N, 68.6-69.9 °W, 9009 km²; CN). The LWR region is located in the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain of the boreal forest (Robitaille and Saucier, 1998), where balsam fir, white birch, white spruce (*Picea glauca*) and black spruce (*Picea mariana*) dominate the landscape with a few deciduous stands composed mainly of trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*) and maples (*Acer spp.*). Mean annual precipitations range between 1000 and 1600 mm annually (Robitaille and Saucier, 1998). The LSJ and CN regions are both located in the black spruce – moss *Bryophyta* domain, where the most common tree species are balsam fir, black spruce, white birch and trembling aspen. Mosses, ericaceous shrubs and forbs mainly compose the understory of the black spruce-moss stands. In both of these regions, mean annual precipitations range between 1000 and 1300 mm annually. While the LWR region is located at a relatively high mean altitude of 853 m with many summits above 1000 m, LSJ and CN regions are characterized by a low rolling topography with respective mean altitudes of 535 m and 495 m (Robitaille and Saucier, 1998). The LWR is divided in two parts by the Highway 75, a four-lane divided road; this area is mainly used for logging and outdoor recreational activities (e.g. hiking, hunting, fishing). The LSJ and the CN regions are essentially uninhabited and support an intensive commercial timber harvest activity.

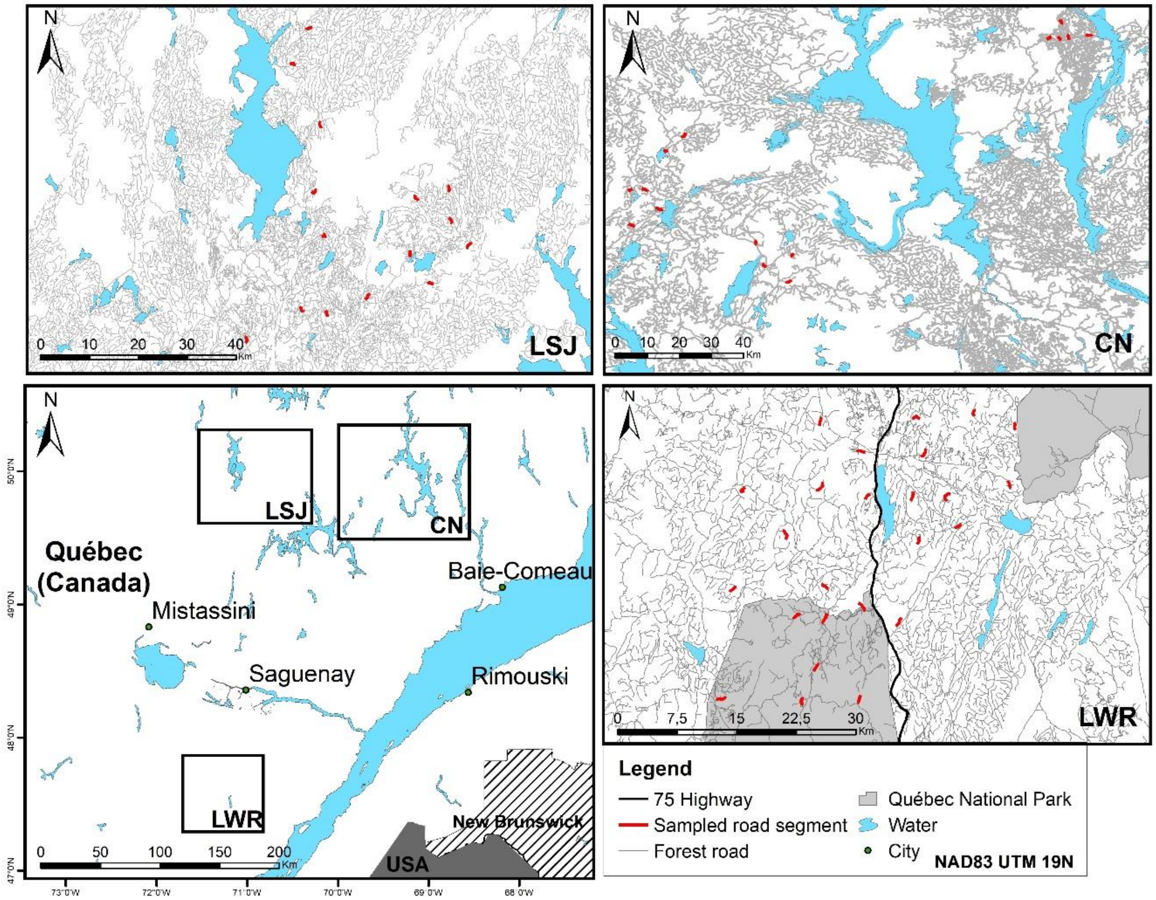

Figure 1.1. Location of sampled logging roads in three different regions (LSJ: Saguenay – Lac-St-Jean, CN: Côte-Nord, LWR: Laurentides Wildlife Reserve) used to study vegetation regrowth on roads in boreal caribou range in Québec, Canada

We used three steps to guide the selection of the different 1-km road segments we studied, using the 1: 20 000 Routard numerical maps published by the Ministère des Forêts, de la Faune et des Parcs du Québec (hereafter MFFP) and based on photointerpretation or aerial survey. First, we sorted all logging roads based on their age (i.e. time since construction). A subset of all roads was then selected based on their accessibility (minimally accessible on foot) and their potential for reclamation to support caribou habitat restoration. To meet this criterion, these roads needed to be no longer used for timber harvesting or to access any industrial, recreational, or touristic facility. Amongst the different 1-km road segments retained by these filters, we selected 56 segments of tertiary logging (unpaved) roads divided into the three regions (26 in the LWR, 15 in LSJ and 15 in CN) and covering an age gradient (0–10 years old: *n*=6, 11–20: *n*=7, 21–30: *n*=13, 31–40: *n*=13, 40+: *n*=17). The availability of road segments in different age categories differed between regions (see Appendix A for the complete distribution of sampled roads per age category in each region). The mean distance between two road segments in a study area was 5.46 ± 2.36 (SD) km with a minimum distance of 1.56 km. In each 1-km road segment, we established 4 sampling plots separated by 250 m in which we characterized vegetation (total of 224 sampling plots; see Figure 1.2 for a schematic visualization of a sampling plot). We conducted our fieldwork between June and August 2019.

Data collection

In each of the 224 sampling plots, we first characterized vegetation regrowth composition (i.e. objective 1) by counting the number of stems per species with a measurable DBH (diameter at breast height, i.e. < 0 cm at 1.30 m from the ground) in two 16-m² circular subplot centered in the middle of the road and separated by 5 m (see Figure 1.2). We summed these counts to obtain the total number of stems per species over the 32-m² area. We decided to use two 16-m² plots and summed their counts instead of doing only one 32-m² plot to avoid including vegetation growing outside of the road segment, i.e. in the road shoulders.

According to Ray (2014), linear features need to be functionally and structurally restored to contribute efficiently to caribou conservation, the goal being to obtain similar densities and species composition of regenerating trees and shrubs than those found in natural, undisturbed stands. We thus characterized the success of vegetation regrowth on logging roads (objective 2) using two different parameters: one referring to the first stage of a successful establishment of vegetation (i.e. *structural* restoration), the other to the constraints imposed by vegetation to predator movement (i.e. *functional* restoration).

Firstly, mean vegetation height is one of the most common regrowth variables used in studies focusing on linear feature regeneration (van Rensen et al., 2015; Dickie et al., 2017; Finnegan et al., 2018; Pigeon et al., 2020), as it provides an approximate index of the return

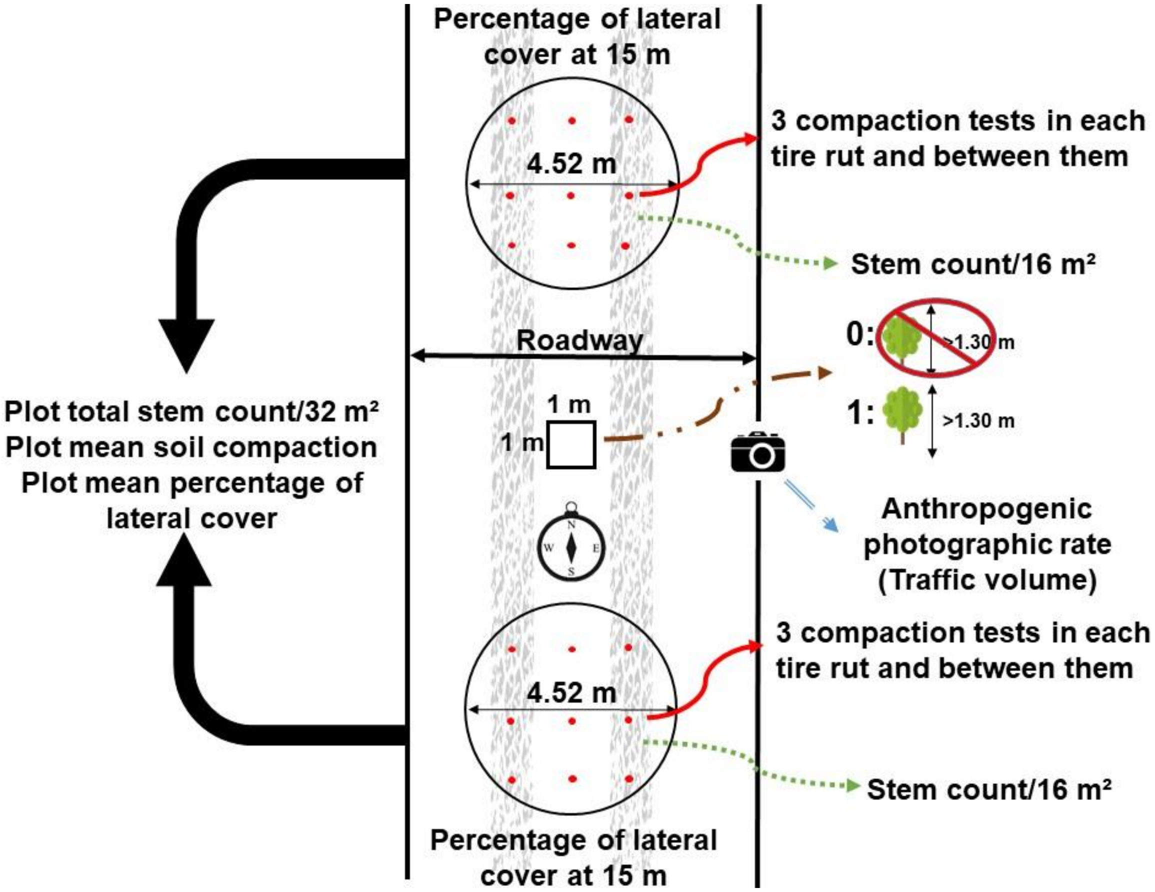

Figure 1.2. Visual representation of each measurement taken in a single sampling plot (4 per road segment) on logging roads in boreal caribou range in Québec, Canada

to a pre-disturbance natural state. We intended to use this variable by measuring the height of each stem, per species and within each plot. However, during data collection, we observed that in our study areas, roads tended to regenerate from the side towards the middle of the roadway, biasing the mean height measurement. In some cases, a plot could have a mean height > 0 even though only 5% of the road surface was covered by vegetation because a few stems grew on the roadside (see Appendix B for examples). This situation was even more obvious in plots with active ATV trails located in the middle of the roadway. Given the potentially misleading outcome of using the mean height, we decided to use the occurrence of at least one stem with a measurable DBH (height >1.30 m) in the middle of the road as a more conservative proxy of regrowth illustrating the beginning of vegetation recovery to pre-disturbance state (*structural restoration*). In each sampling plot, we thus determined the occurrence (i.e. presence or absence) of at least one stem >1.30 m in a 1-m² square subplot centered on the middle of the road, all species considered. We acknowledge that this variable does not represent the return to a pre-disturbance state, but we consider that it represents the first steps toward complete regeneration and argue that factors impeding this early step need to be better understood.

Secondly, one of the most detrimental effects of linear features on caribou demography lies in the facilitation of predator movements on roads (greater speed and prey search efficiency, easier access to previously inaccessible areas) compared to natural stands (Dickie et al., 2017b). As vegetation regrowth on linear structures is commonly dominated by dense shrubs (such as *Alnus spp.* and *Salix spp.*; Finnegan et al., 2019, 2018a), we decided to model the effect of different variables on the percentage (i.e. as a proxy of density) of lateral cover. In each sampling plot, we estimated the lateral cover created by vegetation using a 30 cm x 2 m vegetation profile board located at a 15-m distance from the center of the plot (*sensu* Nudds 1977 as used by St-Laurent et al. 2008 and Leblond et al. 2015) in both directions of the road. We then used these two measurements to calculate each sampling plot's mean lateral cover and used this metric as our second regrowth parameter (*functional restoration*).

We estimated soil compaction using a homemade penetrometer made of a one-end profiled metal rod (1.30 m long, 1 cm of diameter) graduated at every 2.5 cm and a 4.53 kg mass welded to a metal tube. Soil compaction was measured by dropping the 4.53-kg mass on the rod 5 times from a 20-cm height and reading the depth reached by the rod; higher depth values indicated less compacted soil. We took eighteen measurements in each sampling plot, i.e. six in each tire rut and six between them. When tire ruts were not visible, we estimated where they should have been and assessed soil compaction there. In each sampling plot (4 per 1-km road segment), we thus had 18 different compaction measurements that were used to calculate the average plot compaction (see Figure 1.2). We also noted road orientation (in degrees) at each sampling plot. Finally, we installed one motion-activated camera (Moultrie model A-30i) per plot (4 per 1-km road segment) to document the level of human disturbance. We used the software Timelapse2 (Greenberg, 2016) to look at the pictures from these cameras and counted the number of “human events,” i.e. the independent passages of vehicles and ATVs to derive an anthropogenic photographic rate for each plot (i.e. the number of vehicle pictures taken per day; hereafter traffic volume). This variable was integrated in our statistical analyses to evaluate the potential effect of human use on vegetation regrowth.

GIS covariates and data preparation

To account for the potential influence of surrounding roadside stand types on vegetation regrowth of roads, we characterized the landscape around each sampling plot using the 1:20,000 digital forest cover maps provided by the MFFP. These maps were derived from aerial photographs updated in 2016 and have a spatial resolution of 4 ha for forest stands and 2 ha for non-forested areas (e.g., lakes, unproductive lands). We classified land cover types into four categories, i.e. recent cutovers (0–20 years post-logging), deciduous and mixed stands (hereafter deciduous), coniferous stands, and wetlands. We then calculated the proportion of each land cover type category in buffers of different radii (250, 500, 750, 1,000 m) around each plot. We also created a digital elevation model (cell size = 10 x 10 m) to extract elevation and slope at each plot. All spatial analyses and covariate extractions were carried out using ArcGIS 10.1 (ESRI 2012) and R 3.6.1 (R Core Team 2019). We also determined the number of degree-days above 5°C at each plot location using BioSIM (Régnière *et al*., 2012). We used the base temperature of 5°C as this metric base was previously used as a standard by the Atmospheric Environment Service of Environment Canada (Natural Resources Canada, 1981).

Statistical analyses

Determinants of regrowth species composition

We used a canonical correspondence analysis (CCA) to evaluate the relationships between the number of stems per species in each plot and the variables assessed at three scales. At the road-segment scale, the variables considered included soil compaction, road age, orientation, elevation, slope and traffic volume. At the local scale, the variables assessed in the immediate surroundings of the road included the proportion of wetlands, coniferous stands, deciduous stands and 0–20 year-old cutovers calculated in four different buffer radii (250, 500, 750 and 1000 m). Finally, at the landscape scale, the variables considered were latitude, longitude, and the number of degree-days > 5°C. We used a multivariate approach rather than using a univariate analysis to simultaneously consider the interactions between environmental variables and the associations between plant species (Kenkel, 2006). Prior to the analysis, we removed variables contributing to an increase in variance inflation factor > 5 to avoid collinearity. For this analysis only, we removed 50 plots (22%) without stems from the analysis as CCA cannot deal with sampling units with no data (see Zuur et al., 2007). After removing an additional 9 plots with missing data, we ended up conducting the analysis on 165 plots out of the 224 originally sampled. To choose which buffer to use at the local scale, we computed four CCAs using all variables while including only a single buffer size, and chose the buffer included in the CCA explaining the greater proportion of variation for interpretation. We removed elevation and the proportion of cutovers in a 250-m radius due to multicollinearity issues. We used a permutation test to assert the significance of the analysis, axes, and environmental variables. Analyses were conducted in R (R Development Core Team, 2019), using the vegan 2.5-6 library (Oksanen *et al.*, 2019).

Variables influencing regrowth establishment

We used multiple mixed beta regressions (package glmmTMB; Brooks *et al.*, 2017) to model variations in the percentage of lateral cover and mixed logistic regressions (lme4; Bates *et al*., 2015) to model the occurrence of at least one stem >1.30 m in the middle of the road. For both response variables, we built the same set of candidate models based on the hypothesis that three different groups of variables would have an effect on vegetation regrowth variables: road structure, growing conditions and the surrounding environment. In the first model, variables linked to road structure were soil compaction (1/depth reached by the penetrometer), road age (0-10, 11-20, 21-30, 31-40 and 40+ years old), slope, and traffic volume. In the second model, variables referring to growing conditions included the number of degree-days > 5°C, elevation and road orientation (standardized between 0 and 1; van Rensen et al., 2015). The third model included variables characterizing the surrounding environment, namely the respective proportion of wetlands, 0–20-year-old cutblocks, deciduous stands and coniferous stands within a given radius. To determine which radius to use for this environmental model in both analyses, we computed the full model using four different radii (250, 500, 750, 1000 m) and then chose the radius used in the most parsimonious model using the AIC_c (*sensu* Leblond et al., 2011; Lesmerises et al., 2018). We included the number of stems in a plot in all models using the lateral cover as a response variable to control for its effect. We did not build separate models for each region because some age categories were not available for certain regions, unbalancing the sampling design (see Appendix A for age category distribution between regions). Instead, for both dependent variables, we included in each model a PCNM (vector of principal coordinates of neighbour matrices; Borcard and Legendre, 2002) to control for the large-scale spatial autocorrelation pattern that may exist in our dataset (according to Legendre, 1993). In each models, the only significant PCNM was the one at the largest scale and was thus included into each candidate model to account for its cofounding effect. We also included the road segment ID as a random effect to consider the nested design (i.e. four plots nested into a single road segment).

For each response variable, we ranked the 7 candidate models (Table 1.1) using the AIC_c (Burnham and Anderson, 2001). We assessed the fit of the lateral cover models by comparing them to the null model and calculating the marginal R^2 (Nakagawa and Schielzeth, 2013), and used the area under the ROC curve and leave-one-out cross-validation (Pearce and Ferrier, 2000) to validate the models predicting the occurrence of at least one stem >1.30 m. For these two dependent variables, we removed plots with missing measurements and ended up using 215 plots for both analyses out of the 224 plots sampled in the field. Multicollinearity occurred when elevation and the number of degree-days above 5°C were included in the same model. We thus removed elevation from all candidate models for both response variables. The proportion of 0–20-year-old clearcuts and the proportion of coniferous stands in a 500-m radius were correlated when modelling the occurrence of at least one stem >1.30 m; we consequently removed the proportion of 0–20-year-old clearcuts from this analysis. Finally, due to convergence problems when modelling the occurrence of at least one stem >1.30 m, we merged the 0–10 and 11–20 years old age categories and removed the traffic volume covariate as whenever the photographic rate of vehicles was above 0, we found no growing stem in the middle of the road. We conducted all statistical analyses using R 3.6.1 (R Development Core Team, 2019).

Table 1.1. List of candidate models used to model the relationship between lateral cover and the occurrence of at least 1 stem > 1.3 m on logging roads in boreal caribou range in Québec, Canada in 2019. The types of regression used, covariates composing each model, their AIC_c and relative support (ΔAIC_c) are shown. PCNM: vector of principal coordinates of neighbour matrices controlling for spatial autocorrelation, (1|RoadID): random-effect at the road level. See Appendix A for a description, type and range of each covariates.

Response covariate	**Model**	**Explanatory covariates**	**AIC_c**	**ΔAIC_c**	**k**
Lateral cover (%)	1 – Road structure	Age category + Traffic volume + Slope + Soil compaction + log(stem count+1) + PCNM + (1 | RoadID)	-327.9	1.69	6
	2 – Growing conditions	Orientation + degree days + Elevation + log(stem count+1) + PCNM + (1 | RoadID)	-287.3	42.31	5
	3 – Environment	% of deciduous stands + % of coniferous stands + % wetlands + % of clear cuts + log(stem count+1) + PCNM + (1 | RoadID)	-289.9	39.66	6
	4 – Structure + Growing	Model 1 + Model 2	-324.9	4.71	9
	5 – Structure + Environment	Model 1 + Model 3	-329.6	0.00	10
	6 – Growing + Environment	Model 2 + Model 3	-287.9	41.64	10
	7 – Complete	Model 1 + Model 2 + Model 3	-326.2	3.35	13
Occurrence of at least one stem >1.30 m	1 – Road structure	Age category + Slope+ Traffic volume + Soil compaction + PCNM + (1 | RoadID)	166.3	8.09	5
	2 – Growing conditions	Orientation + degree days + Elevation + PCNM + (1|RoadID)	172.9	15.50	4
	3 – Environment	% of deciduous stands+ % of coniferous stands + % wetlands + % of clearcuts +PCNM + (1 | RoadID)	163.3	5.90	5
	4 – Structure + Growing	Model 1 + Model 2	168.1	10.70	8
	5 – Structure + Environment	Model 1 + Model 3	157.4	0.00	9
	6 – Growing + Environment	Model 2 + Model 3	163.7	6.30	8
	7 – Complete	Model 1 + Model 2 + Model 3	160.6	3.20	12

RESULTS

Determinants of regrowth species composition

The canonical correspondence analysis explaining the greater proportion of variance was the one including local-scale variables calculated in a 250-m radius buffer. The CCA was significant (permutation test, *P*<0.001, *n.permutation*=999), as were the first three axes of our model explaining 37.68% of the variation in the number of stems per species between plots. The first axis explained 23.09% of the variation and had an eigenvalue of 0.71, which is higher than the 0.30 value threshold that suggests a strong gradient along that axis (ter Braak and Verdonschot, 1995). In this case, this axis depicts a gradient of adjacent stand composition, from mixed/deciduous on the left to a higher proportion of conifers in a 250-m radius on the right; this gradient mirrors a decreasing gradient of degree-days (> 5°C). The second axis explained 7.97% of the variation and had an eigenvalue of 0.24, suggesting a weaker gradient. This axis represents (from bottom to top quadrants) an increasing proportion of wetlands in a 250-m radius and a decreasing slope. The third and last significant axis had an eigenvalue of 0.20 and explained 6.41% of variation and suggesting a weak gradient. The biplot only shows the first and second axes (Figure 1.3). All covariates used in the model had a significant effect on the number of stems per species (*P*<0.05) except traffic volume and the road orientation.

The number of coniferous stems, especially black spruce and balsam fir, was closely linked to road segments >30 years old, to a higher proportion of coniferous stands in a 250-m radius and to a smaller number of degree-days (> 5°C). A higher number of willows (*Salix spp.*), white birch and aspen stems were found in plots with a steeper slope and surrounded by a lower proportion of wetlands whereas an inverse relationship was found with tamarack (*Laryx laricina*) stems. For all tree species, the number of stems in a plot was negatively influenced by soil compaction and was less abundant on 0–10-year-old road segments except for alders (*Alnus spp.*), which were positively related with these covariates.

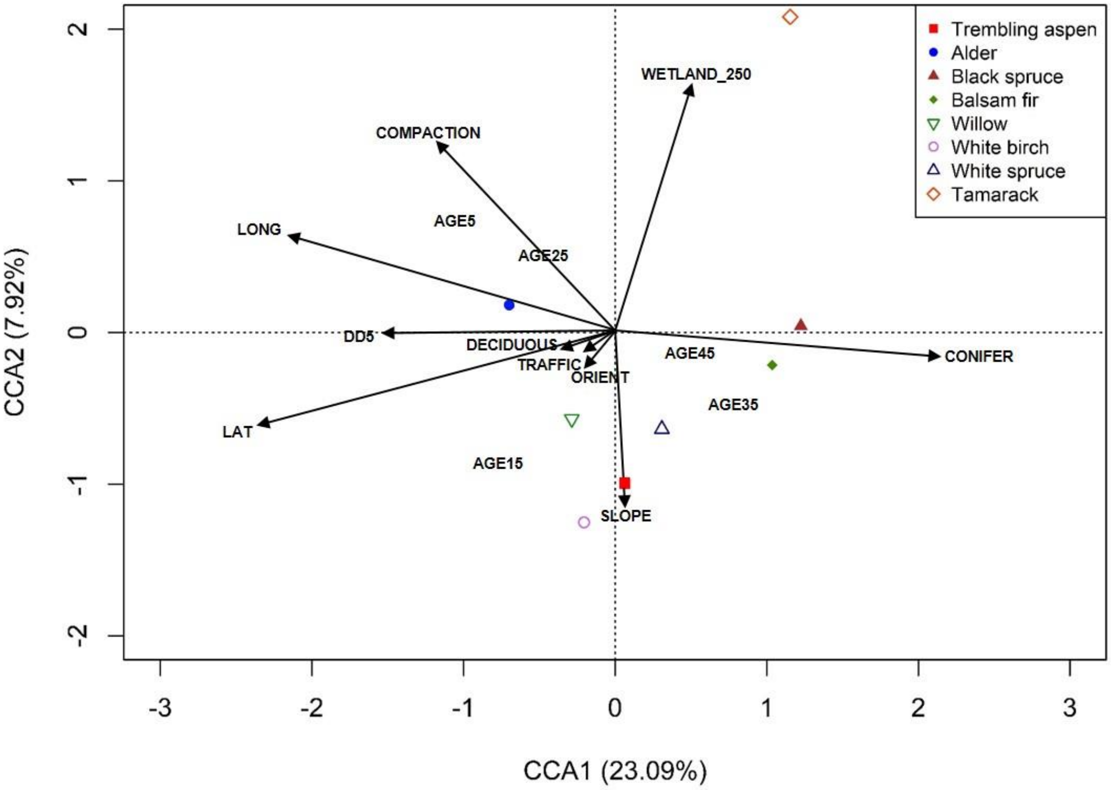

Figure 1.3. First two axes of the canonical correspondence analysis explaining the number of stems per species in relation to different variables hypothesized to have an effect on vegetation regrowth composition of logging roads across boreal caribou range in Québec, Canada (scaling=3). All covariates are significant except traffic volume (TRAFFIC) at the 95% level. The covariates used are longitude (LONG), latitude (LAT), the number of degree-days above 5°C (DD5), road age category, ranging from 0– to 45+ years old (AGE5 to AGE45), the proportion of deciduous stands (DECIDUOUS), coniferous stands (CONIFER) and wetlands (WETLAND_250) in a 250-radius buffer, road orientation (ORIENT) and slope (SLOPE).

Variables influencing regrowth establishment

Lateral cover

The most parsimonious buffer radius used to quantify the influence of environmental covariates was 750 m according to a model selection based on AIC_c. The most parsimonious model explaining variations in lateral cover was model 5, which includes variables referring to road structure and the surrounding environment, although model 1, which contains only road structure variables, received a comparable support ($\Delta AIC_c < 2$, Table 1.1). Compaction had a negative effect on lateral cover in both most parsimonious models (Table 1.2). A greater proportion of wetlands in a 750-m radius had a negative effect on lateral cover in model 5 (structure + environment model). Both models also indicated that there was a positive relationship between the number of stems and lateral cover, and both were different from the null model ($P<0.001$), with a respective R^2 of 0.78 and 0.77 (marginal R^2; Nakagawa and Schielzeth, 2013).

Occurrence of at least one stem >1.30 m

In this analysis, the most parsimonious buffer radius used to quantify the influence of environmental covariates was 500 m according to a model selection based on AIC_c. The most parsimonious model explaining the occurrence of a stem >1.30 m in the middle of the roadway was model 5, which included road structure and environmental covariates (Table 1.1). Road compaction and a higher proportion of deciduous cover in a 500-m radius buffer (centered on a sampling plot) both had a negative influence on the occurrence probability of at least one >1.30 m stem in the middle of the roadway (Table 1.3). The fixed effects (soil compaction, road age, slope, respective proportion of coniferous stands, deciduous stands, and wetlands in a 500-m radius and PCNM) explained 50.8% of the variance (marginal R^2; Nakagawa and Schielzeth, 2013). The best-supported model had a very good fit, with an area under the ROC curve of 0.977, and showed great accuracy with a mean leave-one-out cross-validation accuracy of 89%.

Table 1.2. Most parsimonious mixed beta regression models explaining the percentage of lateral cover on logging roads during the summer of 2019 in boreal caribou range in Québec, Canada. Covariates are presented with their coefficient (β) and 95% confidence interval (95% CI). Significant parameters are highlighted in bold. 0–10-year-old category was used as the reference category for the age covariate. PCNM: vector of principal coordinates of neighbour matrices controlling for spatial autocorrelation. See Appendix A for description, type and range of each covariates.

Covariates	**Structure**		**Structure + Environment**	
	β	**95% CI** [Lower : Upper]	**β**	**95% CI** [Lower : Upper]
Traffic volume	0.126	[-0.130 : 0.382]	0.083	[-0.174 : 0.340]
Compaction	**-0.543**	**[-0.800 : -0.287]**	**-0.538**	**[-0.793 : -0.283]**
Age15	-0.501	[-1.576 : 0.572]	-0.513	[-1.650 : 0.623]
Age25	-0.725	[-1.715 : 0.264]	-0.705	[-1.735 : 0.326]
Age35	-0.476	[-1.485: 0.533]	-0.451	[-1.603: 0.701]
Age45	-0.456	[-1.463 : 0.550]	-0.338	[-1.534 : 0.857]
Slope	-0.029	[-0.182 : 0.124]	-0.060	[-0.214 : 0.094]
Coniferous750	-	-	-0.347	[-0.810 : 0.115]
Deciduous750	-	-	-0.206	[-0.491 : 0.079]
0-20 Clearcuts750	-	-	-0.433	[-0.932 : 0.066]
Wetlands750	-	-	**-0.310**	**[-0.531 : -0.090]**
Log(Total stem count+1)	**0.880**	**[0.716 : 1.043]**	**0.865**	**[0.704 : 1.027]**
PCNM	0.206	[-0.032 : 0.444]	0.203	[-0.079 : 0.485]

Table 1.3. Covariates, unstandardized beta coefficient (β) and their 95% confidence interval (95% CI) of the most parsimonious mixed logistic regression model explaining the occurrence of at least one stem >1.30 m at the center of the plot on logging roads during the summer of 2019 in boreal caribou range in Québec, Canada. Significant coefficients are highlighted in bold. 0–20-year-old category was used as the reference category for the age covariate. PCNM: vector of principal coordinates of neighbour matrices controlling for spatial autocorrelation. See Appendix A for description, type and range of each covariates.

Covariates	**β**	**95% CI**
		[Lower : Upper]
Compaction	**-1.432**	**[-2.479 : -0.385]**
Age25	1.429	[-2.235 : 5.092]
Age35	1.675	[-2.711: 6.062]
Age45	4.319	[-0.311 : 8.949]
Slope	-0.174	[-0.881 : 0.533]
Coniferous500	0.460	[-1.093 : 2.012]
Deciduous500	**-2.356**	**[-4.208 : -0.504]**
Wetlands500	0.216	[-0.588 : 1.021]
PCNM	-0.475	[-1.661 : 0.710]

DISCUSSION

In line with our objectives of describing how and why vegetation regrowth can re-establish itself on logging roads following forest harvesting, we showed that the surrounding environment and road soil compaction were important drivers of regrowth species composition and affected the probability of occurrence of finding regenerating stems on the road. We discuss the importance of these results in a context of caribou conservation.

Determinants of regrowth species composition

The strong gradient illustrated by the first axis represented a variation in the number of degree-days above 5 °C that mirrors a variation in the proportion of coniferous stands surrounding the road segment. This suggests that the surrounding environment (i.e. surrounding landscape and forest cover attributes) plays an important role in determining which plant species will recolonize the roadway. Along this gradient, coniferous stems, especially black spruce stems, were more abundant in plots located on older (30–40 and 40+ years old) road segments that experience a lower number of degree-days during the growing period. Inversely, younger and more compacted roads built in regions that experience a higher number of degree-days were more likely to be colonized by alder stems and less likely by coniferous stems. In the LWR region, which experiences the lowest mean number of growing degree-days (mean value of 1228 DD ± 55 (SD)) (Natural Resources Canada, 1981) due to its relatively high mean elevation, alders were almost absent (i.e. found in only ~3% of the plots, for 12 stems total; Appendix A). Inversely, alders were much more frequently found in LSJ (i.e. in 43% of the plots, for a total of 363 stems) and CN (69% of the plots, 1593 stems; Appendix A) regions that both benefit from a greater total heat available for plant growth (mean value (±SD); LSJ: 1496 (±100) DD, CN: 1426 DD (±103)).

Alders and other deciduous shrubs are known to grow faster near gravel roads, forming a closed canopy quite quickly that prevents moss, sphagnum moss and lichen growth (Myers-Smith et al., 2006; Gill et al., 2014), thus competing with coniferous tree species regeneration (Jobidon, 1995). Since mosses represent one of the most optimal seedbeds for black spruce (Pothier, 2000; Greene et al., 2004; Lavoie et al., 2007), conditions favoring alder growth, in this case a higher number of growing degree-days and a more compacted roadway, likely prevents the establishment of black spruce stems on road segments.

Along the first-axis gradient, coniferous stems (mainly black spruce and balsam fir) were also found to be more abundant on roads surrounded by a higher proportion of coniferous stands (assessed in a 250-m radius). This result corroborates the findings of Lieffers et al. (2017), who noticed that the density and size of nearby seed sources were some of the most important factors determining the density of conifer seedlings on oil drilling pads in western Canada. Boreal coniferous species have a very poor seed survivability post-abscission and, consequently, aerial seedbanks play an important role in the recolonization of disturbances (Fraser, 1976; Greene et al., 1999). Thus, our results suggest that the retention of coniferous stands in close proximity to logging roads appears to be an important factor to consider if these segments are to regenerate naturally after forest harvesting and reach a pre-disturbance composition.

The second axis represented a gradient of increasing slope and decreasing proportion of wetlands (bog, fen, marsh) in the close surroundings (a 250-m radius) of a road segment. This suggests that the level of drainage could influence the tree species composition of regrowth on logging roads. Tamarack stems were more abundant in plots located in sites characterized by a gentle slope, while deciduous species, especially white birch, typically grew on roads found in areas with a steeper slope. Tamarack is a tree species known to grow in a wet environment that has a thick layer of organic soil (Lecomte and Bergeron, 2005), and since stems growing near a disturbance play an important role in the re-establishment of natural regeneration (Lieffers et al., 2017), roads surrounded by a greater proportion of wetlands were more likely colonized by tamarack. Inversely, white birch is known to grow on steeper slopes (Couillard et al., 2016), which aligns with our findings.

Our results also show that under certain conditions, vegetation regrowth on logging roads can potentially shift toward alternate succession trajectories: some roads were increasingly colonized by deciduous species instead of coniferous species, which can be found in a pre-disturbance state. This phenomenon appeared to be more present in the CN region, where the number of deciduous stems was still important on older (40+ years old) roads while the number of coniferous stems remained fairly low regardless of age categories (Appendix A). Such a shift toward deciduous regrowth is of concern for caribou conservation as it could potentially benefit to alternative prey and, consequently, wolf and black bear (Finnegan et al., 2018a, Tatterstall et al., 2020). Moreover, 22% of all sampling plots had no stems growing on the road. Although the majority of these empty plots were on roads < 20 years old, 18 (36%) of them were on roads >30 years old (Appendix A), underlying the possible need to manually plant trees on these roads that fail to regenerate naturally. Shift in successional trajectories has also been suggested in the case of seismic lines as species composition can differ from the forest interior and remain in early successional stages composed of forbs and shrubs (Lee and Boutin, 2006; Dabros et al., 2018; Finnegan et al., 2018a). Similarly to our results, seismic lines with no regrowth were also common even decades after their construction (Lee and Boutin, 2006).

Soil compaction as a driver of regrowth establishment

Road compaction appears to have a very important influence on the establishment of regrowth on logging roads as it had a significant negative effect on both regrowth variables used in this study. This result is consistent with the widely documented negative effects of soil compaction on forest regrowth (see Cambi et al., 2015 for an extensive literature review). Compaction increases soil bulk density by reducing the size of air-filled pores (McNabb et al., 2001), thus limiting the soil oxygen and water content available for root growth (Startsev and McNabb, 2000; Smith et al., 2001). Compaction also increases mechanical resistance, limiting roots and consequently tree regrowth (Clark et al., 2003; Blouin et al., 2005). To our knowledge, this is the first time that the direct relationship between soil compaction of linear features and regrowth in caribou range is made empirically. Our findings are in accordance with previous studies that indirectly demonstrated the negative effect of compaction on the mean height of vegetation regrowth on linear features. Indeed, Pigeon et al. (2016) and Hornseth et al. (2018) showed that mean vegetation height was lower when off-highway vehicle use of seismic lines was more important, which they partly interpret as a result of increased soil compaction. Similarly to their findings, we also showed that the use of roads by vehicles appeared to have a negative effect on regrowth, as whenever the traffic volume was above zero, there was never a growing stem in the center of the road.

The role of the surrounding environment in regrowth establishment

The proportion of wetlands found in the surroundings of roads had a negative effect on the density of lateral cover in one of our candidate models, suggesting that roads built in an environment with relatively poor drainage suffer vegetation regrowth problems that could prevent the growth of a dense lateral cover. This result could be attributed to relatively poor growing conditions for black spruce on road segments found in poor-drainage conditions. In our study areas, black spruce is the main species growing in wetlands, along with tamarack (Robitaille and Saucier, 1998), and roads increasingly surrounded by wetlands are thus also surrounded by a greater amount of black spruce. As trees in close proximity to a disturbance play an important role in the density of seedlings on disturbances (Lieffers et al., 2017), black spruce stems seem to be the species most likely to colonize roads in wet sites. However, black spruce seedling establishment and growth are known to be optimal in the moist seedbed layers provided by the mineral horizon with pioneer moss coverage (Fleming and Mossa, 1994; Charron and Greene, 2002) as well as in sites with complex microtopography (Roy et al., 1999; Lieffers et al., 2017; Filicetti and Nielsen, 2020). Therefore, a flattened road surface offering poor water penetration and retention capacities due to heavy compaction (Startsev and McNabb, 2000) is not suitable for black spruce growth. We noted that such conditions often resulted in cleared (no vegetation) road segments in wetter areas of the landscape.

Other studies conducted in western Canada on seismic lines also noted poorest regrowth on lines located in lowland and wet ecosites using parameters such as height and growth (van Rensen et al., 2015; Finnegan et al., 2019). In these studies, differences in height were mainly attributed to a modification in hydrological conditions such as a high water table and soil depression on wet seismic lines, which make the soil more prone to flooding (van Rensen et al., 2015). This mechanism seems unlikely to occur on forest roads considering that the methods used to build them in wetter areas are specially designed to limit “water contamination” (Ordre des ingénieurs forestiers du Québec, 2009) and maintain a solid structure to allow timber extraction. This supports our interpretation regarding the relative unsuitability of road surface for black spruce growth as the preferred explanation for the sparse lateral cover observed on roads in wetter environments in our study areas. The differences in road construction techniques aiming at limiting water contamination in poorly drained terrains could also have been responsible for poor regrowth establishment. However, little information was available in our study areas about the specific techniques used for each individual road segment with regards to terrain conditions, and we could thus not test for such a potential confounding effect.

The proportion of mixed/deciduous stands in close proximity appears to have a negative effect on the probability of counting at least one stem >1.30 m at the center of a road segment in our study area. However, this result might be an artifact induced by the way we stratified stands adjacent to our sampling plots, as the deciduous category regrouped deciduous and mixed stands ≥ 20 years old. Of the 8858 polygons found in this category, 51% were between 20 and 40 years old, 21% between 40 and 60 years old and 28% were ≥60 years old. In comparison, the age distribution of the polygons in the coniferous stand category was much more evenly distributed. Hence, the lower probability of counting at least one stem in the middle of a road when the proportion of deciduous and mixed stands is higher in the surroundings of a plot could be a result of too short a time interval for deciduous trees to reach maturity, colonize the center of the roadway and grow to a height ≥1.30 m.

Management implications for the recovery of threatened boreal populations of woodland caribou

Our study highlights the importance of considering multiple scales (road segments, the local surroundings of the road and over larger landscapes) when studying the establishment of vegetation regrowth on logging roads as species composition varies across gradients embedded in these spatial scales. Because the reclamation of linear features is costly (Filicetti et al., 2019), it is virtually impossible to restore all logging roads found within a caribou population range. Consequently, land use managers should aim to reclaim road segments that fail to provide characteristics known to constrain the movements of predators, mainly wolves, as well as their potential attractiveness for alternative prey (moose and deer) and opportunistic predators (bears). Since roads that cross a greater proportion of wetlands provided a sparser lateral cover in our regions, we advocate that these roads should be prioritized for active restoration efforts (unpacking the soil and planting; Lacerte et al., 2021). This recommendation is supported by observations made by Dickie et al. (2017a, 2017b), as sparser vegetation is hypothesized to increase wolf hunting efficiency, resulting in increased boreal caribou mortality, and by DeMars and Boutin (2018), who reported that linear features located in lowlands are selected by wolves and bears, thus offering an easy access to caribou spatial refugia. This recommendation, however, considers only the role of linear features on predator movements; we thus stress that restoration of caribou habitat will require a multifaceted approach that considers a wide array of characteristics (*sensu* Ray, 2014; e.g. understory regrowth, forage available to alternative prey, tree height) that were not considered in our study.

Our results also identified soil compaction as the primary hindrance of regrowth establishment, lateral cover and the occurrence of at least one stem >1.30 m, supporting the need to unpack the soil when road reclamation is the goal. Mechanical decompaction techniques such as mounding and ripping have the potential to revert the effects of compaction on seed establishment and growth (Filicetti et al., 2019) but would also re-establish a complex microtopography beneficial to coniferous regrowth (see Lacerte et al., 2021). The retention of coniferous trees in close proximity to roads as well as the planting of coniferous species also seems necessary to guarantee a coniferous regrowth on logging roads. If necessary, future road development in caribou range should employ techniques known to limit soil compaction and vegetation damage, such as the use of winter roads that requires little to no excavation work because of the augmented bearing capacity of the frozen soil. Finally, further studies should investigate how fine-scale characteristics of roads influence their use by caribou, wolf, black bear and moose, as previous research often only included logging roads as a single or limited (e.g. unpaved/paved roads) number of categories in studies focusing on large mammal use of roads (e.g. Whittington et al., 2005; Laurian et al., 2008; Mosnier et al., 2008; Leblond et al., 2013).

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APPENDIX A. ADDITIONAL INFORMATION ON SAMPLED ROAD SEGMENTS, COVARIATES AND COMPOSITION OF VEGETATION REGROWTH

Table A.1. Covariates used in the canonical correspondence analysis modelling the number of stems per species that are growing on logging roads across boreal caribou range in Québec, Canada

Covariate	Description	Type and range
Road-scale		
CAT_AGE	Time since road construction	Categorical with 5 levels: 0-10 (Age5), 11-20 (Age15), 21-30(Age25), 31-40 (Age35), 40+ (Age45) years old
COMPACTION	Measurement of soil compaction (1/depth reached by the penetrometer)	Continuous positive [0.026 : 0.400]
SLOPE	Slope at each plot	Continuous positive [0.00 : 19.21]
TRAFFIC	Number of vehicle and ATV photos/Effort	Continuous [0.00 : 1.71]
ORIENT	Road orientation standardized between 0-1	Continuous [0 : 1]
ELEVATION	Elevation (m)	Continuous [217 : 1023]
Local-scale		
0-20 clearcuts250	Proportion of 0-20 year-old clearcuts (%) in a buffer of 250-m radius	Continuous [0 : 100]
CONIFEROUS	Proportion of >20 year-old coniferous stands (%) in a buffer of 250-m radius	Continuous [0.00 : 99.99]
DECIDUOUS	Proportion of >20 year-old deciduous stands (%) in a buffer of 250-m radius	Continuous [0.00 : 85.73]
WETLAND_250	Proportion of wetlands (%) in a buffer of 250-m radius	Continuous [0 : 23.96]
Landscape-scale		
LONG	Longitude NAD83 UTM 19N	Continuous [312101.8327 ; 527648.4219]
LAT	Latitude NAD83 UTM 19N	Continuous [524697.382 ; 5583674.399]
DD5	Number of degree-days >5°C	Continuous [1103 : 1616]

Table A.2. List of covariates used in the different mixed beta regression models used to explain variations in the percentage of lateral cover on logging roads across boreal caribou range in Québec, Canada

Covariate	Description	Type and range
Road structure		
CAT_AGE	Time since road construction	Categorical with 5 levels: 0-10 (Age5), 11-20 (Age15), 21-30(Age25), 31-40 (Age35), 40+ (Age45) years old
Compaction	Measurement of soil compaction (1/depth reached by the penetrometer)	Continuous positive [0.026 : 0.400]
Slope	Slope at each plot	Continuous positive [0.00: 19.21]
Traffic	Number of vehicle and ATV photos/Effort	Continuous [0.00 : 1.71]
Surrounding Environment		
0-20 Clearcuts 750	Proportion of 0-20 year-old clearcuts (%) in a buffer of 750-m radius	Continuous [0 : 91.76]
Coniferous 750	Proportion of >20 year-old coniferous stands (%) in a buffer of 750-m radius	Continuous [0.00 : 96.12]
Deciduous 750	Proportion of >20 year-old deciduous stands (%) in a buffer of 750-m radius	Continuous [0.00 : 47.62]
Wetlands 750	Proportion of wetlands (%) in a buffer of 750-m radius	Continuous [0 : 10.31]
Growing conditions		
Degree days > 5°C	Number of degree-days above >5°C	Continuous [1103 : 1616]
Orientation	Road orientation	Continuous [0 : 1]
All model		
Log(stemcount+1)	Sum of stems in 32 m² (log-scale)	Continuous [0:3.224]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.956 : 1.05]
(1|RoadID)	Random effect at the road-level	Categorical with 56 levels

Table A.3. List of covariates used in the three different mixed logistic regression models used to explain the variation in occurrence of a stem >1.30 m on logging roads across boreal caribou range in Québec, Canada

Covariate	Description	Type and range
Road structure		
CAT_AGE	Time since road construction	Categorical with 4 levels: 0-20 (Age15), 11-20 (Age15), 21-30(Age25), 31-40 (Age35), 40+ (Age45) years old
Compaction	Measurement of soil compaction (1/depth reached by the penetrometer)	Continuous positive [0.026 : 0.400]
Slope	Slope at each plot	Continuous positive [0.00 : 19.21]
Traffic	Number of vehicle and ATV photos/Effort	Continuous [0.00 : 1.71]
Surrounding Environment		
0-20 Clearcuts 500	Proportion of 0-20 year-old clearcuts (%) in a buffer of 500-m radius	Continuous [0 : 96.04]
Coniferous 500	Proportion of >20 year-old coniferous stands (%) in a buffer of 500-m radius	Continuous [0.00 : 99.39]
Deciduous 500	Proportion of >20 year-old deciduous stands (%) in a buffer of 500-m radius	Continuous [0.00 : 62.71]
Wetlands 500	Proportion of wetlands (%) in a buffer of 500-m radius	Continuous [0 : 14.75]
Growing conditions		
Degree days > 5°C	Number of degree-days above >5°C	Continuous [1103 : 1616]
Orientation	Road orientation	Continuous [0 : 1]
All model		
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.956 : 1.05]
(1|RoadID)	Random effect at the road-level	Categorical with 56 levels

Table A.4. Breakdown of sampled logging road segments into age categories (no. of years since construction) and regions (CN: Côte-Nord, LSJ: Saguenay-Lac-St-Jean, LWR: Laurentides Wildlife Reserve) across boreal caribou range in Québec, Canada

Region	Age category					
	0-10	**11-20**	**21-30**	**31-40**	**40+**	**Total**
CN	4	7	0	0	4	15
LSJ	0	0	2	8	0	10
LWR	13	8	3	0	1	25
Total	17	15	5	8	5	50

Table A.5. Breakdown of sampling plots with no growing stem in a 32-m² surface into age categories (no. of years since construction) and regions (CN: Côte-Nord, LSJ: Saguenay-Lac-St-Jean, LWR: Laurentides Wildlife Reserve) across boreal caribou range in Québec, Canada

Region	Age category					
	0-10	**11-20**	**21-30**	**31-40**	**40+**	**Total**
CN	2	4	4	0	5	15
LSJ	1	1	3	7	3	15
LWR	3	2	6	6	9	26
Total	6	7	13	13	17	56

Table A.6. Total number of stems per species growing in plots on logging roads in three different regions (CN: Côte-Nord, LSJ: Saguenay-Lac-St-Jean, LWR: Laurentides Wildlife Reserve) across boreal caribou range in Québec, Canada. The column Stems refers to the sum of stems counted in each sampling plot, while the column Occurrence represents the percentage of plot with at least one stem present

	CN		LSJ		LWR	
Species	Stems	Occurrence (%)	Stems	Occurrence (%)	Stems	Occurrence (%)
Alnus sp.	1674	72	363	43	12	4
Salix sp.	144	33	154	38	33	15
Betula papyrifera	43	17	143	30	21	7
Populus tremuloides	6	8	42	25	0	0
Picea mariana	25	13	122	43	707	69
Abies balsamea	39	13	102	42	338	42
Picea glauca	0	0	26	22	5	5
Laryx laricina	0	0	12	5	83	13

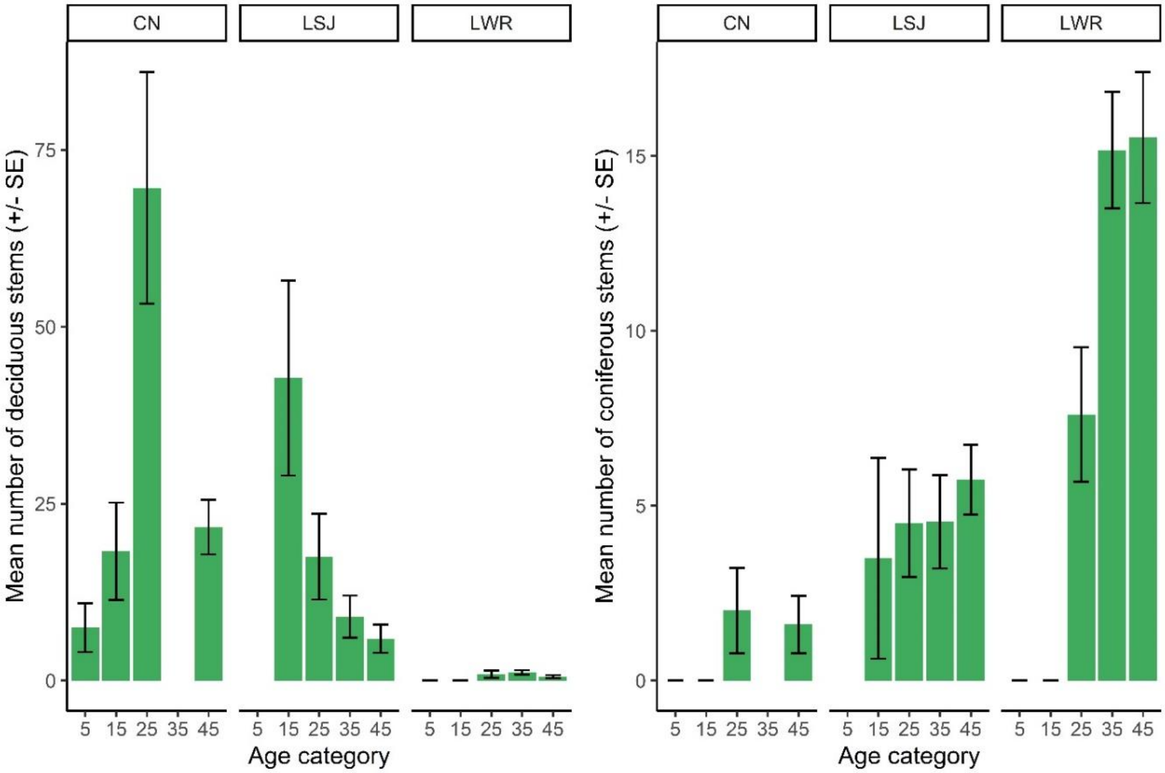

Figure A.1. Mean (± standard error) number of deciduous and coniferous stems counted on logging roads of different ages in three different regions across boreal caribou range in Québec, Canada. CN: Côte-Nord region, LSJ: Saguenay-Lac-St-Jean region, LWR: Laurentides Wildlife Reserve. Age categories refer to 0-10 (5), 11-20(15), 21-30 (25), 31-40 (35), and 45 (40+) year-old roads

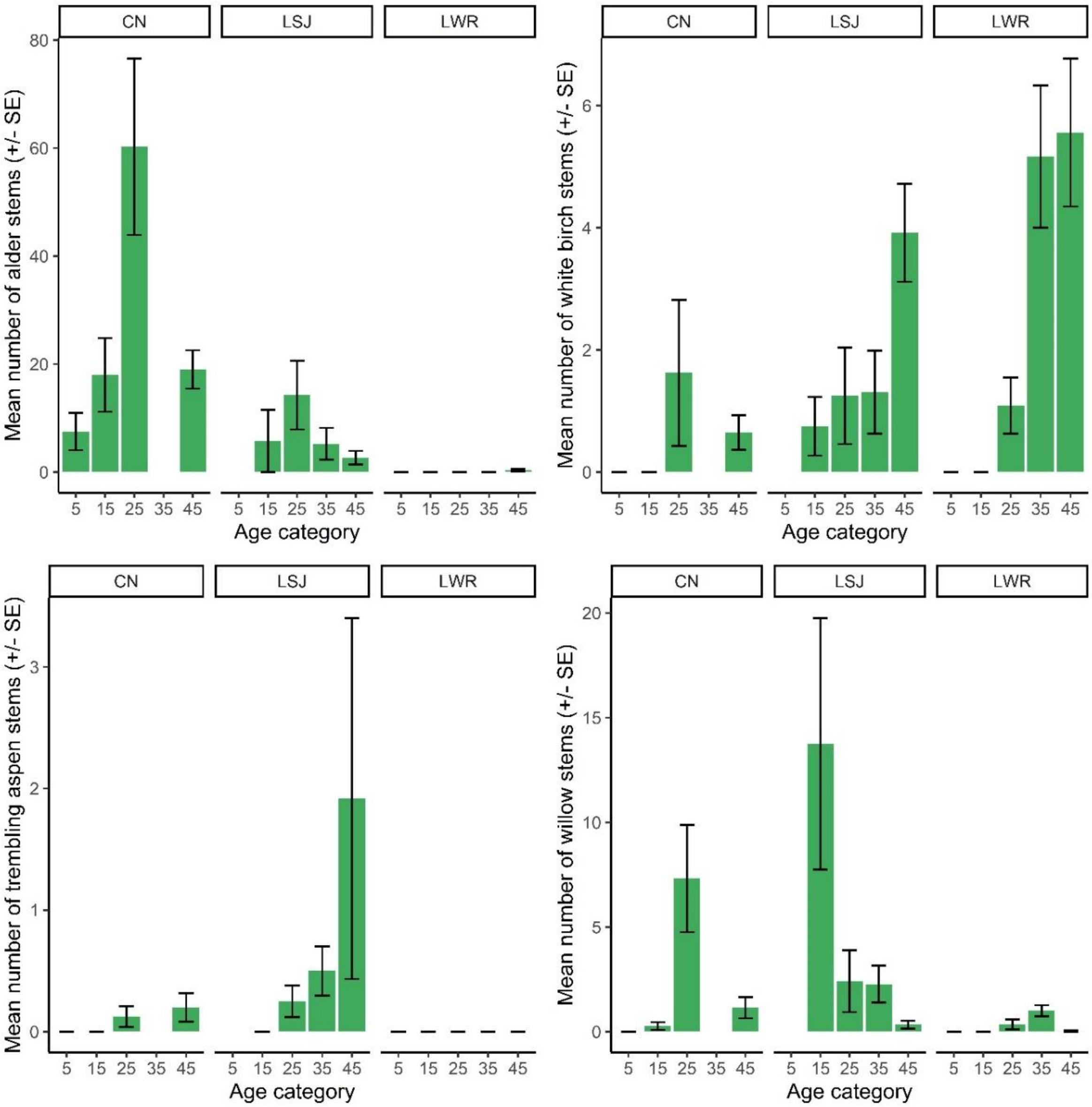

Figure A.2. Mean (± standard error) number of stems per deciduous species counted on logging roads of different ages per region across boreal caribou range in Québec, Canada. CN: Côte-Nord region, LSJ: Saguenay-Lac-St-Jean region, LWR: Laurentides Wildlife Reserve. Age categories refer to 0-10 (5), 11-20(15), 21-30 (25), 31-40 (35), and 45 (40+) year-old roads

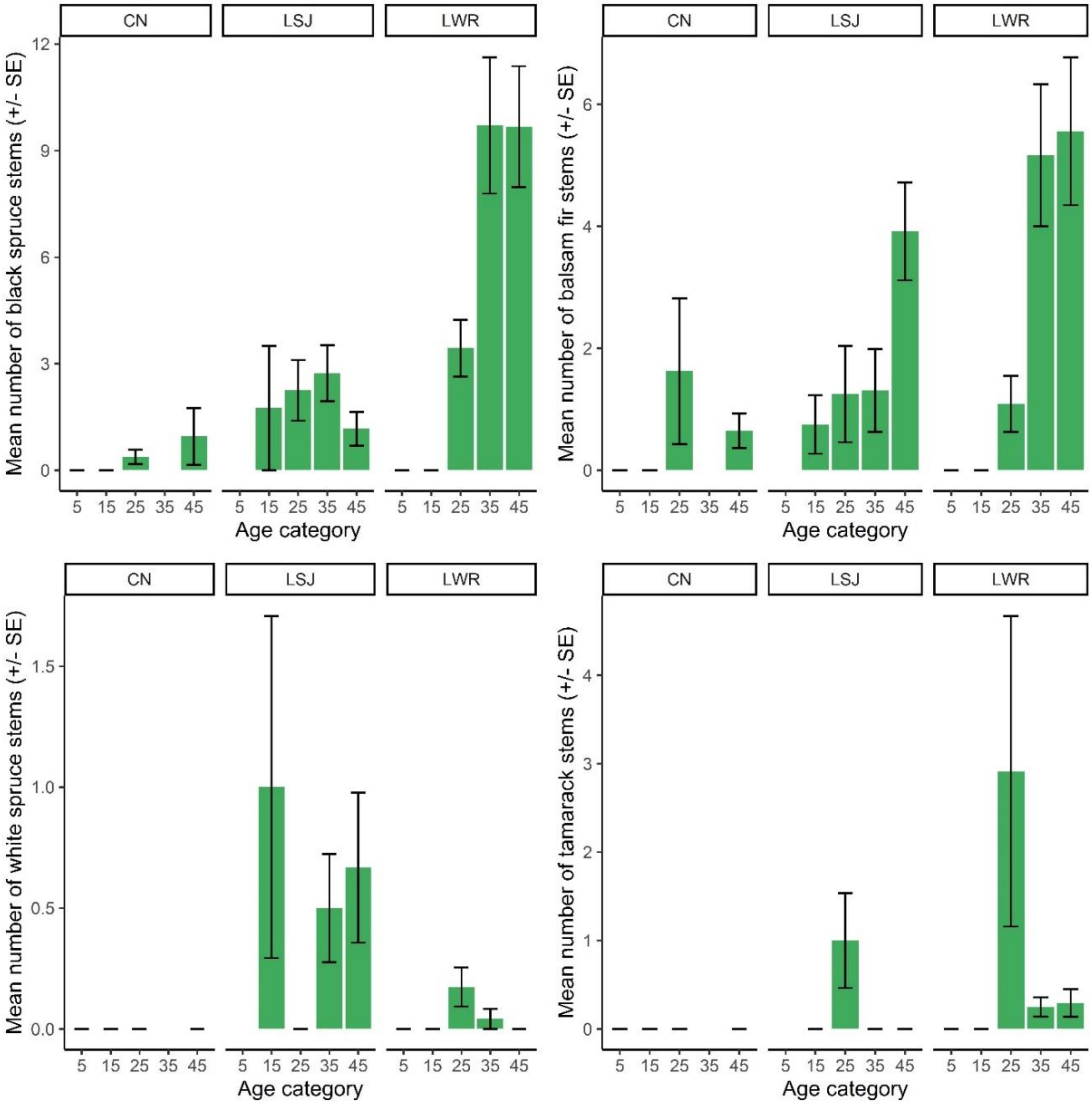

Figure A.3. Mean (± standard error) number of stems per coniferous species counted on logging roads of different ages per region across boreal caribou range in Québec, Canada. CN: Côte-Nord region, LSJ: Saguenay-Lac-St-Jean region, LWR: Laurentides Wildlife Reserve. Age categories refer to 0-10 (5), 11-20(15), 21-30 (25), 31-40 (35), and 45 (40+) year-old roads

APPENDIX B. EXAMPLE OF A CASE WHERE MEAN VEGETATION HEIGHT WAS NOT A SUITABLE REGROWTH PARAMETER IN THE PRESENT STUDY

In this example, both pictures were taken from plots with a similar mean height (1.70 m and 1.76 m). Even if both plots have very different regrowth, they have a similar mean height due to roadside regrowth in the first case. Using the occurrence of a stem >1.30 m in a plot centered in the middle of the road instead of the mean height allowed us to effectively discriminate these plots and model a conservative proxy of road reclamation.

Fig B.1. Pictures of two different plots with the same mean height

CHAPITRE 2

STAIRWAY TO HEAVEN OR HIGHWAY TO HELL? RÔLE DES CARACTÉRISTIQUES DES CHEMINS FORESTIERS SUR LEUR UTILISATION PAR LES GRANDS MAMMIFÈRES EN FORÊT BORÉALE

2.1 RÉSUMÉ EN FRANÇAIS DU DEUXIÈME ARTICLE

Devant l’accroissement global des perturbations anthropiques qui menace de plus en plus la biodiversité, des méthodes de conservation comme la restauration d’habitats dans des paysages perturbés apparaissent de plus en plus incontournables. La mise hors service des structures anthropiques linéaires et la restauration d’habitats favorables sont parmi les principales mesures à considérer pour le rétablissement des populations de caribou forestier (*Rangifer tarandus caribou*). Cependant, restaurer activement l’habitat sur toutes les perturbations linéaires retrouvées dans l’habitat du caribou s’avère impossible et déterminer le rôle des différentes caractéristiques de ces perturbations sur leur utilisation par les prédateurs et les compétiteurs du caribou pourrait permettre d’établir un ordre de priorité. Par conséquent, le but de cette étude était de déterminer l’influence des caractéristiques des chemins forestiers sur leur niveau d’utilisation par le loup gris (*Canis lupus*), l’ours noir (*Ursus americanus*), l’orignal (*Alces americanus*) et le caribou. Nous avons utilisé des modèles linéaires généralisés mixtes pour relier l’utilisation des chemins faite par le loup, l’ours, l’orignal et le caribou, estimé à l’aide de pièges photographiques, à des variables à l’échelle du chemin tout en considérant des variables du milieu environnant. La probabilité qu’un chemin soit utilisé par le loup était plus grande lorsqu’un chemin était entouré d’une plus grande proportion de milieux humides et lorsque la densité de couvert latéral sur le chemin était faible. L'intensité d'utilisation par l'ours était plus faible lorsque les chemins étaient plus âgés (20+ ans) comparativement à ceux âgés de 0-10 ans et plus élevée lorsque les chemins étaient entourés d'une plus grande proportion de forêts résineuses. L'utilisation faite par l'orignal était plus importante lorsque les chemins étaient dans la catégorie d'âge 11-20 ans et lorsqu'ils étaient entourés d'une plus faible proportion de parterres de coupes récentes (0-20 ans). Nous n'avons pas pu tester l'utilisation du caribou en raison d'un trop faible nombre de données. Nos résultats soulignent l'importance de considérer autant les variables à l'échelle du chemin que le contexte paysager dans lequel les chemins forestiers sont bâtis afin de prioriser ceux dont les caractéristiques sont les plus problématiques pour le caribou et ainsi orienter efficacement les efforts de restauration de son habitat.

Mots-clés *:* Perturbation humaine, Relation prédateur-proie, Chemin forestiers, Caribou forestier, Perturbation linéaire, Forêt boréale

Ce deuxième article, intitulé « *Stairway to heaven or Highway to hell? How characteristics of logging roads shape their use by large mammals in the boreal forest* », a été corédigé par moi-même ainsi que par les professeurs Pierre Drapeau et Martin-Hugues St-Laurent. Cet article sera soumis à la revue avec comité de révision par les pairs *Biological Conservation*. En tant que premier auteur, ma contribution à ce travail a été l'essentiel de la recherche, du développement de la méthode, de l'exécution des analyses et de la rédaction de l'article. Les professeurs Martin-Hugues St-Laurent et Pierre Drapeau ont fourni l'idée originale et coordonné l'élaboration du projet, assuré son financement en plus d'avoir révisé et commenté les analyses et le texte de l'article.

2.2 STAIRWAY TO HEAVEN OR HIGHWAY TO HELL? HOW CHARACTERISTICS OF LOGGING ROADS SHAPE THEIR USE BY LARGE MAMMALS IN THE BOREAL FOREST

ABSTRACT

Habitat restoration in disturbed landscapes is a key conservation measure that helps reduce the ever-increasing impacts of anthropogenic disturbances on biodiversity. The decommissioning of anthropogenic linear features and the restoration of suitable habitat are top priorities for the recovery of the threatened populations of boreal caribou (*Rangifer tarandus caribou*). However, the decommissioning of all linear features found in caribou range is impossible, and determining which characteristics make them more beneficial to caribou predators and competitors could assist in prioritizing those that may be most critical for boreal caribou habitat restoration. We thus aimed to determine how fine-scale logging road characteristics influence their use by gray wolf (*Canis lupus*), black bear (*Ursus americanus*), moose (*Alces americanus*) and caribou. We used generalized linear mixed models to test the effect of road-scale characteristics on the use of logging roads by wolves, bears and moose while also considering larger-scale covariates. Wolves had a greater probability of using roads surrounded by wetlands and for which the lateral cover density was low. For bears, the intensity of use was lower on 20+ year-old roads when compared to 0–10-year-old roads and higher on roads surrounded by coniferous stands. Moose intensity of use was higher on 11–20-year-old and lower on 30+ year-old roads and decreased on roads surrounded by clearcuts and with a lower number of deciduous stems. We could not test for caribou use as we did not capture enough events. Our study highlights the importance of considering both road-scale characteristics and the landscape context in which roads are built to prioritize the most detrimental roads to caribou conservation and orient efficient restoration efforts of its habitat.

Keywords*:* Human disturbance, Predator-prey relationship, Logging road, Boreal caribou, Linear feature, Boreal forest

INTRODUCTION

Biodiversity loss represents one of the greatest challenges of the Anthropocene era (Pimm et al., 2014; Steffen et al., 2011), and current extinction rates are now approaching those of past mass extinction events (Barnosky et al., 2011, 2012). Recent conservation efforts are still deemed insufficient to reverse the effects of the main drivers of biodiversity loss (Hoffmann et al., 2010), namely anthropogenic habitat loss, overexploitation and invasive species, but also geological and climate change (Purvis et al., 2000). Ecosystems are increasingly impacted by anthropogenic disturbances, and some are even being pushed outside of their natural range of variability (Cyr et al., 2009; Drapeau et al., 2009; Seidl et al., 2016). Therefore, the restoration of disturbed landscapes is essential to re-establish key functional or ecological conditions (Perring et al., 2015; Suding, 2011).

The boreal populations of woodland caribou (*Rangifer tarandus caribou*; hereafter caribou) are currently listed as Threatened under the Species at risk Act in Canada (Species at Risk Act, 2002), and most populations are currently in decline (Environment Canada, 2011). During the past decades, several studies have shown that this decline is mainly driven by the expansion of anthropogenic disturbances encroaching on caribou habitat (e.g. COSEWIC, 2014; Environment Canada, 2011; Festa-Bianchet et al., 2011; Johnson et al., 2015; Rudolph et al., 2017; Stewart et al., 2020; Vors and Boyce, 2009). Among all anthropogenic disturbances, timber harvesting converts late-seral forest stands, known to be favorable to caribou, into early-seral stands preferred by alternative prey such as moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*) (Dawe et al., 2014; Mumma et al., 2021). The increased access to abundant, palatable, energy- and protein-rich foraging resources triggers an increase of alternative prey densities that, in turn, support larger gray wolf (*Canis lupus*; hereafter wolf) densities that can jeopardize caribou persistence via higher predation pressure (Wittmer et al., 2007, 2005) through a complex trophic relationship called apparent competition (sensu Holt, 1977; see also DeCesare et al., 2010; Frenette et al., 2020). Regenerating vegetation found in recent cutblocks is also profitable to black bears (*Ursus americanus*) as it provides plenty of high-quality food items that are otherwise scarce in the boreal forest (Mosnier et al., 2008). Although black bears feed mostly on plants (Lesmerises et al., 2015; Raine and Kansas, 1990; Romain et al., 2013), they are efficient opportunistic predators of ungulate calves (Murrow et al., 2009; Patterson et al., 2013; Popp et al., 2018; Vreeland et al., 2004). Throughout Canada, black bears were identified as an important mortality agent for caribou calves (Mahoney et al., 2016; Mumma et al., 2019a; Pinard et al., 2012). Anthropogenic linear features such as seismic lines—narrow corridors built for energy exploration—and logging roads were shown to be selected by predators (Dickie et al., 2017a; Tigner et al., 2014; Wittische et al., 2021), increasing their movement rate and travel speed (Dickie et al., 2017b), which results in higher encounter rates with prey, and, consequently, greater predation on caribou (Leblond et al., 2013; Mumma et al., 2017; Whittington et al., 2011). The combination of all these behavioral responses to a changing landscape following anthropogenic disturbances is currently the main hypothesis used to explain the decline of boreal caribou populations in Canada (Hervieux et al., 2013; Johnson et al., 2020).

The decommissioning of linear features and habitat restoration represent one of the top priorities for caribou conservation (Hervieux et al., 2013; Johnson et al., 2019; McKay et al., 2021). Linear feature decommissioning can be either slow and passive, where the regeneration of vegetation on logging roads (St-Pierre et al., 2021) or seismic lines (Finnegan et al., 2018a; Van Rensen et al., 2015) is initiated by natural recolonization from adjacent shrubs and trees, or it can be active, which can involve road closure, soil decompaction and tree planting (Tattersall et al., 2020a; Lacerte et al. 2021). However, as the active restoration of linear features can be costly (Filicetti et al., 2019; Johnson et al., 2019), it is virtually impossible to reclaim all anthropogenic linear features in caribou range. Consequently, determining which characteristics of linear features make them more or less attractive to predators and alternative prey is essential to establish an order of priority.

A growing number of studies described several aspects of the use of anthropogenic linear features by wolves in caribou range, such as wolf-caribou encounters (Mumma et al., 2017; Whittington et al., 2011), linear feature selection by wolves (DeMars and Boutin, 2018;

Dickie et al., 2017a; Kittle et al., 2017), and characteristics impeding wolf travel speed (Dickie et al., 2017b; Finnegan et al., 2018b). However, relatively few studies have described the use of linear features by black bears (but see DeMars and Boutin, 2018; Tigner et al., 2014) and moose (but see Dickie et al., 2020; Mumma et al., 2018), and the ones that did often focused on seismic lines in western Canada. A small number studied use of logging roads (e.g.; Leblond et al., 2013; Muhly et al., 2019; Mumma et al., 2019b), and often used a rather limited classification of roads (e.g. unpaved/paved roads), using tools such as resource selection functions (RSF, Manly et al., 2002) and step selection functions (SSF, Fortin et al., 2005) at a relatively large scale. However, not all logging roads are the same: they can be located in different environments (e.g. successional forest stages) or have different intrinsic characteristics (e.g. varying compaction, St-Pierre et al., 2021). Logging roads with sparser regrowth could be more attractive to wolves as they facilitate movement (Dickie et al., 2017a), while roads with a well-established deciduous regrowth could provide food items for black bears and moose (Finnegan et al., 2019, 2018a) and consequently be more used by these species. Co-use by interacting species could also play a role in one's use of a road: linear features can be perceived as a predation risk by prey (Dickie et al., 2020; Leclerc et al., 2014), so roads increasingly used by predators could be less used by caribou and moose. As such, distinguishing how the intensity of use of logging roads varies in relation with varying fine-scale characteristics could help further identify which roads should be restored, and therefore appears to be of paramount importance for caribou conservation.

In this study we document the effect of different logging road fine-scale (i.e road level) characteristics on the intensity of use by wolves, black bears, moose and caribou. We also test the effect of large-scale variables known to influence responses of large mammals to roads. We hypothesize that roads providing characteristics known to facilitate movements will be selected by wolves. Accordingly, we predict that the intensity of use of a road by wolves will be more important when the percentage of lateral cover is lower. Because black bears and moose are known to select for abundant forage, we hypothesize that they would both be attracted by logging roads offering an easy access to food items. We predict that the intensity of use by these species will be greater on younger roads with a greater herbaceous cover for black bears, and more deciduous stems for moose. However, since moose could perceive roads used by wolves, its main predator, as risky, it could consequently balance forage accessibility with predation risk. If so, we predict that moose intensity of use will be negatively related to wolf use. Finally, as caribou avoid linear features, where the probability of encountering a predator is higher, and usually stay away from alternative prey (Peters et al., 2013), we expect that caribou intensity of use will be lower on roads frequented by other species.

MATERIALS AND METHODS

Study area

Our study area was divided into 3 different regions on the north shore of the St. Lawrence River in Québec, Canada (Figure 2.1). The southernmost region encompasses the Laurentides Wildlife Reserve, and the northern part of the Jacques-Cartier provincial park (47.3-47.7°N, 71.0-71.5°W, 2,120 km²; hereafter LWR) and is located in the range of the Charlevoix caribou population. The second region is located in northern Saguenay-Lac-St-Jean, in the Portneuf and Piraube caribou population ranges (49.7-50.3°N, 70.6-71.2°W, 3,900 km²; LSJ). Finally, the third region covers the northwestern part of the Côte-Nord and is part of the Manicouagan caribou population range (49.6-50.5°N, 68.6-69.9°W, 9,009 km²; CN). These three regions encompass two boreal bioclimatic domains. The LWR region is comprised in the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain, the LSJ region is located at the limit of the balsam fir-white birch and black spruce (*Picea mariana*) – moss *Bryophyta* domain and the CN region is located in the black spruce – moss domain (Robitaille and Saucier, 1998). Mature stands in the LWR are mostly composed of coniferous trees such as balsam fir, black spruce, and white spruce (*Picea glauca*) found in pure stands or with boreal deciduous species, mainly white birch and trembling aspen (*Populus tremuloides*). LSJ is mostly dominated by black spruce combined with a mix of the above-mentioned species, with a feathermoss understory cover typical of

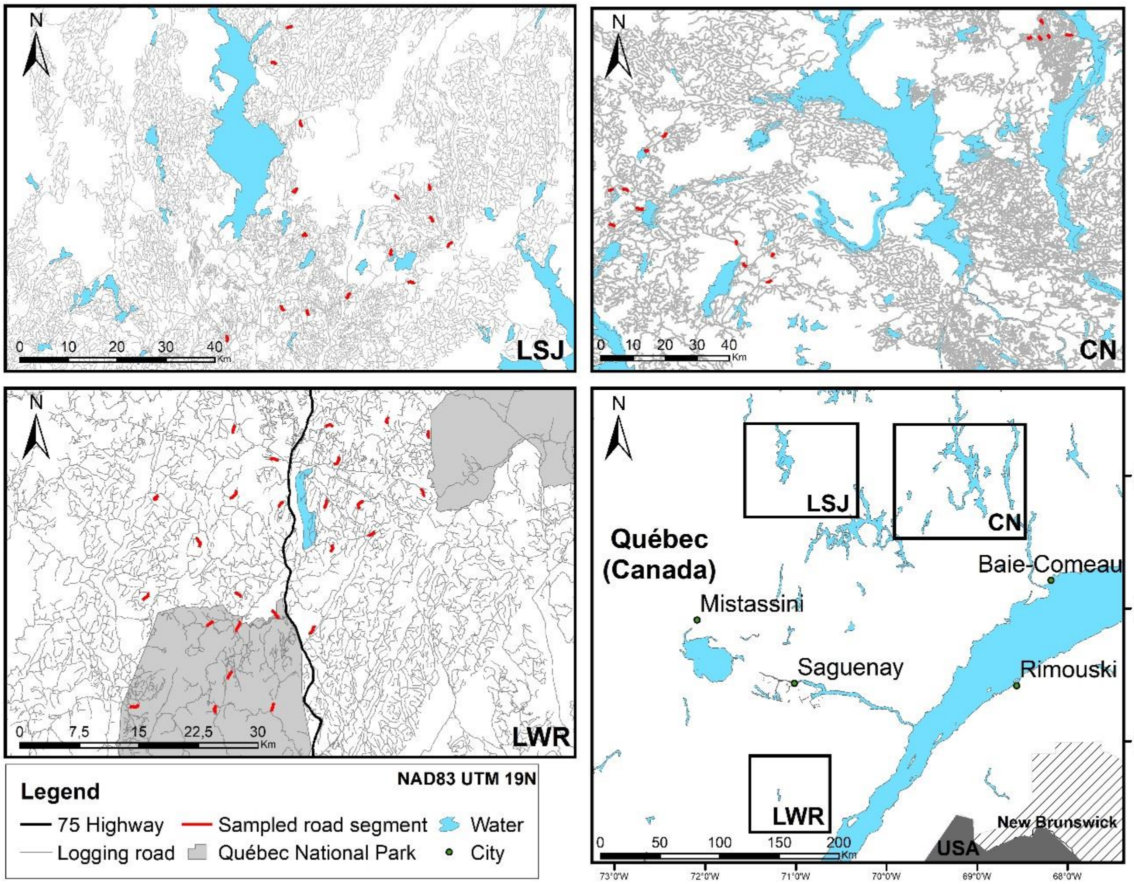

Figure 2.1. Distribution of sampled logging road segments across three regions (LWR: Laurentides Wildlife Reserve, LSJ: Saguenay – Lac-St-Jean, CN: Côte-Nord) in boreal caribou range in Québec, Canada

the black spruce-moss domain (Robitaille and Saucier, 1998). Pure black spruce stands dominate the landscape in the CN region with an understory mainly composed of mosses and ericaceous shrubs. At time of data collection (2018-2020), each of the three regions were used for intensive commercial logging and comprised recent and regenerating clearcuts. While the mean elevation is high in the LWR region (853 m), both the LSJ and CN regions have a relatively low mean elevation (respectively 535 m and 495 m). LSJ and CN are located more than 100 km north of the nearest towns and are essentially uninhabited and human presence in mainly due to resource extraction activities, whereas the LWR region is crossed by the 75 Highway and used for both commercial logging and recreational activities (hiking, fishing, camping). According to the Environment Canada (2011), total disturbance levels reach 80% in LSJ, 82% in the LWR and 32% in CN.

The large mammal community is similar across the three regions: caribou and moose are the main large prey species while gray wolves and black bears are the main predators. Data on wolf, black bear and moose densities are scarce. No estimate of wolf density exists in Québec, while black bear density estimates vary and are estimated to be 0.24 bear/10 km² in LWR, 0.33-0.93 bear/10 km² in CN and 0.41-1.32 bear/10 km² in LSJ. Moose density was estimated to be 0.209 moose/km² in the southern part of the LWR region (in the Jacques-Cartier provincial park) but are thought to be currently lower. Moose density estimates based on hunting statistics vary between 0.1-0.2 moose/km² in LSJ and 0.05 to 0.24 moose/km² in CN (Ayotte and Chenel, 2018).

The Charlevoix caribou population is a small population undergoing continuous declines with an estimate of 31 individuals in 2019 and approximately 23 individuals in 2020 (Hins and Rochette, 2019, 2020). Caribou densities are 0.6 caribou/100 km² in the LSJ region (Plourde et al., 2020) and are estimated to range between 1.2-2.1 caribou/100 km² in the CN region (Heppell, 2020).

Sampling design and data collection

We selected 56 1-km logging (unpaved) road segments (excluding winter roads) following a three-step selection process and using 1 : 20 000 Routard numerical maps published by the Ministère des Forêts, de la Faune et des Parcs du Québec (hereafter MFFP). All logging roads were first sorted by their time since construction (hereafter age) into five categories: 0–10, 11–20, 21–30, 31–40 and 40+ years old (0 years old representing roads built the same year the selection process took place i.e. 2018). A subset of roads was then selected based on their accessibility (i.e. relative proximity to passable road networks). Only roads that could potentially be reclaimed for caribou habitat restoration were selected; these roads needed to be no longer used for timber harvesting or to access recreational, touristic, or industrial facilities. These last two criteria were assessed by photointerpretation or following an aerial survey conducted by the MFFP. We ended with 7 road segments that could be accessed by vehicle, 25 by ATV (max distance traveled = 10 km) and 24 on foot (max distance traveled = 1 km). The mean distance between two road segments was 5.46 ±2.36 (SD) km with a minimum distance of 1.56 km and a maximum of 12.65 km.

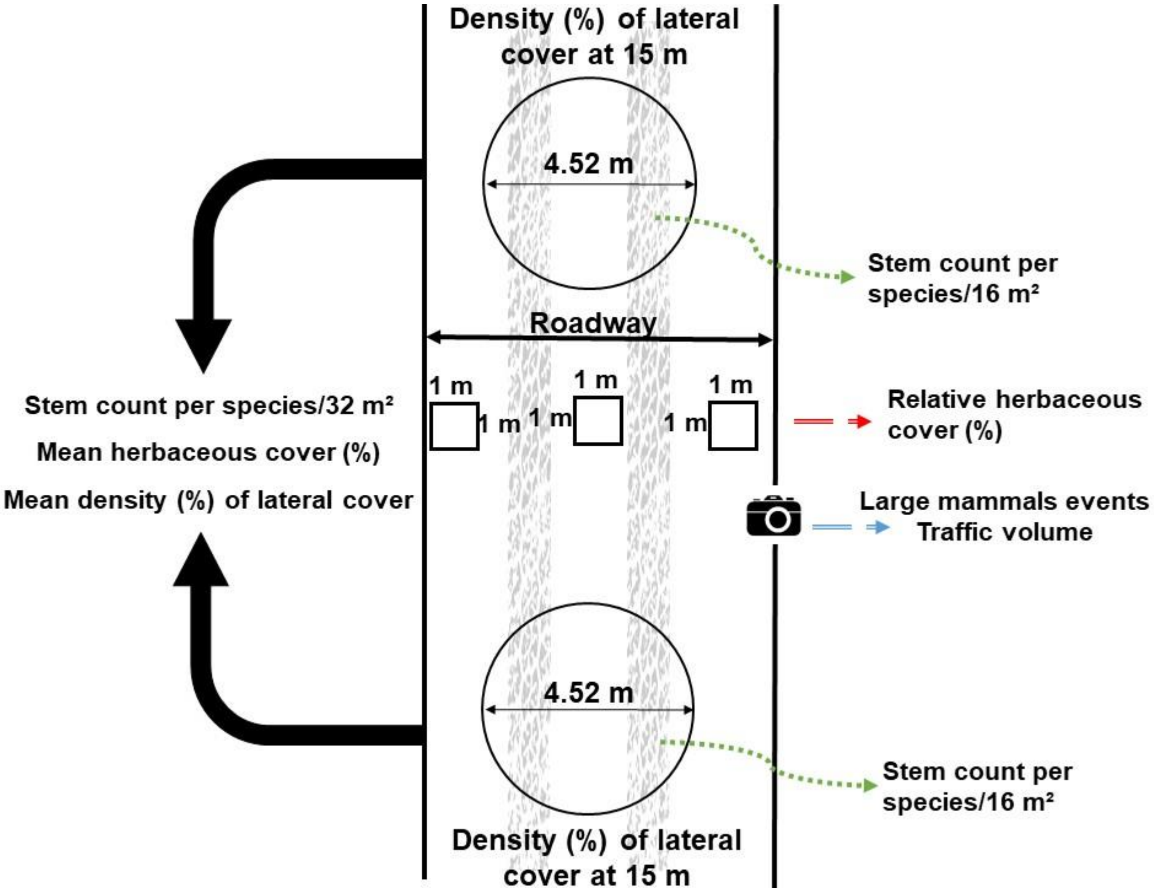

Figure 2.2. Visual representation of each measurement taken at a camera station (4 per road segment) on logging roads in boreal caribou range in Québec, Canada

On each road segment, we established 4 stations separated by 250 m. In each station, we installed a motion-activated camera (Moultrie model A-30i) facing the roadway diagonally (4 per 1-km segment, 220 in total) and ensured that any movement occurring from one side to the other of the road could activate the sensor. We also installed two motion-activated cameras (110 in total) at random locations 300 m away each road segments (hereafter adjacent forest); their data were later used to estimate local densities (see section 2.3.1). We fixed each camera at a height at which all target species would be detected (~1-1.4 m). Each camera (roadside and random) was set at a 3-photo burst per detection mode with a 15 sec interval between detection. At each adjacent forest camera, we measured the detection zone to later derive the detection angle necessary to estimate densities (Appendix D). Cameras were active from early June to mid-September during three consecutive summers (2018, 2019 and 2020).

In 2019, we measured different covariates at each camera station to include them in our statistical analyses as independent variables. At each roadside camera station, we counted the number of stems with a measurable diameter at breast height (>0 cm at 1.3-m height above ground level; hereafter DBH) per species in two 16-m² circular plots and summed them to get a number of stems per 32 m² (see details in St-Pierre et al., 2021). We also determined the relative percentage of cover of herbaceous vegetation in three 1-m² quadrats (one on each side and one in the middle of the roadway; Figure 2.2) and calculated the mean coverage for the entire camera station. Finally, we estimated the density (percentage) of lateral cover at a 15-m distance in both directions parallel to the road using a 30 cm x 2 m vegetation profile board (*sensu* Nudds, 1977 as used by St-Laurent et al., 2008; Leblond et al., 2015) and calculated the mean density of lateral cover for the camera station.

Data preparation

Camera trapping data

We used the Timelapse2 software (Greenberg, 2016) to classify each photo taken by the cameras. An event was noted whenever a caribou, moose, wolf or black bear activated a camera. If multiple individuals of the same species triggered a camera at the same time, we considered that the number of events equaled the number of individuals observed (following Keim et al., 2019). For example, if two moose individuals were caught on the same picture, the number of events was considered to be two. To avoid the potential bias of counting the same individual twice on two photos, we considered any animal photographed in a 30-min time-lapse to be the same (as used by Tattersall et al., 2020a, 2020b). For each camera placed along a road segment, this gave us the number of events per species. We also noted the number of photos of ATVs and vehicles and summed their count to get a proxy of traffic volume of each segment. We noted the number of days during which each camera was active to account for the difference in sampling effort between cameras. We excluded cameras with an effort <10 days as they were often malfunctioning and considered unreliable.

Lele et al. (2013) pointed out the confusion in the use of different terms and concepts (e.g. occupancy, use, selection, choice) in habitat and resource selection studies and the need to define clearly what is being measured, and in which specific unit and during which specific time period. In our case, we were interested in the intensity of use of logging roads by large mammals rather than the probability of selection or occupancy. We thus defined the intensity of use as the number of events per species (i.e. frequency of use) of a camera station (specific unit) during a data collection season (time period). We used the intensity of use per species as a response covariate in a generalized linear mixed modeling (GLMM) framework (Sollmann, 2018; Tattersall et al., 2020a). Despite the potential limitations related to this approach (e.g. imperfect detection rate) that are normally accounted for by using occupancy modeling (see MacKenzie et al., 2002; Sollmann, 2018), we deemed it to be sufficiently robust to meet our objective. A companion study (Gagnon-Labrosse et al., unpublished data) tested the detection rate of multiple camera-trap models at different camera heights, animal speeds and distances from the camera using domestic species of different sizes. Preliminary results suggested that the camera model we used did not miss any animal passages at an 8-m distance and only missed 3.3% of events at a distance of 15 m. Because the mean width of logging roads sampled in this study averaged between 6–8 m and cameras were placed diagonally to maximise the distance during which an animal traveled in front of a camera, we considered that the potential bias in detection rates was low. Moreover, several recently published studies were successful to describe animal activity using the raw or transformed number of events as proxy (Heim et al., 2017; Keim et al., 2019; Tattersall et al., 2020a, 2020b).

The number of events detected by each adjacent forest camera and the mean number of individuals per event were used to derive an approximate regional density of each species per region per year. We estimated densities using the random encounter model (Rowcliffe et al., 2008). We estimated black bear and moose travel speed using GPS telemetry data used in previous studies in the LWR and LSJ regions (Leblond et al., 2010; Massé et al., 2014). We could not estimate local densities for wolves and caribou due to the low number of animals photographed on adjacent forest cameras.

GIS Data

To account for the potential effect of the roads' surrounding environment on their use by large mammals, we used the 1: 20,000 digital forest cover maps published by the MFFP and characterized the landscape around each camera station. These maps are derived from aerial photographs, were updated in 2016, and have a spatial resolution of 4 ha for forest stands and 2 ha for non-productive areas (e.g. lakes). We categorized the landscape into four landcover types: recent cutovers (0–20 years post-logging), wetlands (marsh, bog, fen), mixed and deciduous stands (20+ years old; hereafter mixed), and coniferous stands (20+ years old). We calculated the proportion of each landcover type in buffers of different radii (250, 500, 750, 1000 m) centered on the camera station. We also calculated road density in these same buffers. Finally, for each camera station, we extracted the slope, the distance to the closest permanent water body, longitude and latitude.

Statistical analyses

According to our hypotheses, we built a model with road-scale variables describing ease of movement for wolves, and another model including vegetation variables associated with forage availability for black bears and moose, and a co-use model for each species (see Appendix C; Table C.1., C.2. and C.3). The combinations of variables included in each model vary and are described below for each species. We also built models for each species at a larger scale using anthropogenic footprint and surrounding habitat covariates that have already been shown to influence selection of linear features by large mammals (Beauchesne et al., 2013; Latham et al., 2011; Mumma et al., 2019; Newton et al., 2017; Tigner et al., 2014). Covariates included in the anthropogenic footprint model were road density and the proportion of 0–20-year-old clearcuts in the surroundings of a camera. Habitat covariates were the proportion of mixed stands, coniferous stands, wetlands and the distance to the nearest permanent water body. We then tested each model and their combinations (total of 15 models, see Appendix C; Table C.1, C.2, C.3) and selected the most parsimonious one using the AIC_c (Burnham and Anderson, 2001). We used the buffer radius that best explained the observed variation using the AIC_c (*sensu* Lesmerises et al., 2018) to calculate the proportion of each covariate (0-20-year-old clearcuts, wetlands, mixed stands, and coniferous stands) as well as road density. The assumptions of our statistical models were verified using the DHARMa package (Hartig, 2020). Because we captured too few pictures of caribou during the three years of survey, we could not build models to test our hypotheses for this species.

Due to our zero-inflated dataset for wolves, we could not test for the intensity of use and thus recoded event counts into binary (0/1) data to test the effect of covariates on the probability of use in a mixed logistic regression (library lme4; Bates et al., 2015), where the probability of use is defined as the use of a camera station at least once during the data collection season. The first candidate model contained variables known to ease movement: road age, slope, and the density (percentage) of lateral cover. Co-use model covariates included traffic volume (log-scale) and use by moose and black bears. We assessed model fit using a leave-one-out cross-validation, the area under the ROC curve (AUC) and by comparing the model to the null model.

We modeled the intensity of use by black bears using a mixed negative binomial regression (package glmmTMB; Brooks et al., 2017). The covariates used in the forage accessibility model were road age, slope, density of lateral cover, and the mean cover of herbaceous species. Co-use model covariates included traffic volume (log-scale) and use by moose and wolves. We also used a mixed multiple negative binomial regression to describe the effect of different covariates on the intensity of use by moose. Forage accessibility covariates included road age, slope, density of lateral cover (in %) and forage availability (the summed abundances of trembling aspen, white birch and willow stems at each camera station). We included a quadratic term to better describe variation in forage availability (following the observed distribution of residuals). Co-use covariates were traffic volume (log-scale) and use by wolves and black bears. We compared the model to the null model and calculated the marginal R^2 for both moose and black bear models.

To account for the spatial autocorrelation that often occurs at different scales in natural systems (Legendre, 1993), we used a principal coordinate of neighboring matrix (PCNM; Borcard and Legendre, 2002) analysis. The only significant PCNM was the one at the largest scale and was thus included into each candidate model to account for its confounding effect (see St-Laurent et al., 2007, 2008 for example). We also included road ID-year as a random factor in each model to account for pseudoreplication problems (Hurlbert, 1984). In all models, we included the regional density of moose or black bear. Finally, the effort (i.e. the number of days a camera was active) was included as a fixed effect in the logistic regressions for wolves and as an offset in the negative binomial models for black bears and moose. All analyses were conducted using R 4.0.3 (R core team, 2019).

RESULTS

The total sampling effort over the three consecutive summers was 58,035 camera-days for cameras placed alongside a road segment (mean of 92 days per camera per year) and 29,656 camera-days for adjacent forest cameras in adjacent forest (mean of 90 days per camera per year). The most photographed species (on roads: R; adjacent forest: AF) was moose (R: 3614 events; AF: 277) followed by black bear (R: 1866; AF: 115), wolf (R: 1125; AF: 6) and caribou (R: 36; AF: 9) (Appendix C Table C.7).

The probability of use of roads by wolves was best explained by model 12 (road-scale + habitat) although models 1, 3 and 8 received comparable support ($AIC_c < 2$; Appendix C Table C.1). As model 12 includes all the covariates used in models 1, 3 and 8, we only retained model 12 for further interpretation (Table 2.1). The probability of using a road was lower when the density of lateral cover was high and when the road was surrounded by a lower proportion of wetlands (in a 500-m radius), but higher when traffic volume and use by black bears and moose were high (Table 2.1). Finally, a greater sampling effort increased the probability of photographing at least one wolf and the PCNM was significant. The model was significantly different from the null model ($P < 0.001$), had an area under the ROC curve of 0.955, a mean leave-one-out cross-validation accuracy of 0.78 and a R^2 of 0.20.

The top-ranking models explaining the black bear intensity of use were model 3 (road-scale) and model 12 (road-scale + habitat; AIC_c <2; Appendix C, Table C.2). We only interpret the result of model 12 (Table 2.1) because model 3 is nested in model 12. Black bear intensity of use was lower on roads in the 21–30, 31–40 and 40 + year-old categories compared to roads aged 0–10 years, and lower when traffic volume was high and when a road was surrounded by a lower proportion of coniferous stands (in a 250-m radius). Black bear intensity of use and wolves use were also positively correlated. The PCNM was also significant. The model was different from the null model and had a marginal R^2 of 0.26.

Moose intensity of use was best explained by model 11, which included road-scale and surrounding habitat covariates, and by model 7 (Forage availability + habitat; AIC_c <2; Appendix C Table C.3), which is nested in model 11; we thus only interpret model 11 (Table 2.1). Moose used more 11–20 year-old roads and less 31–40 and 40+ year-old roads compared to the 0–10 year-old category. We found a quadratic relationship between moose intensity of use and forage availability; the intensity of use was greater when forage availability was increased until a threshold above which an increase in forage availability had no further effect on the intensity of use by moose. We also noted that moose intensity of use of a road was positively linked with wolf use, and influenced by a lower proportion of 0–20 year-old cutblocks surrounding the road (in a 250-m radius) and by a higher moose density.

The PCNM was also significant. This model was different from the null model ($p<0.001$), and the marginal effects explained 31% of the variation (R^2 of 0.31).

Table 2.1. Most parsimonious mixed regression models explaining wolf probability of use, and black bear and moose intensity of use of logging roads during the three consecutive summers of 2018-2020 in boreal caribou range, Québec, Canada. Covariates are presented with their coefficient (β) and bootstraped 95% confidence interval (95%CI). Significant covariates are highlighted in bold. The 0-10-year-old category was used as reference category for the age covariate. PCNM: vector of principal coordinates of neighbour matrices controlling for spatial autocorrelation. The effort was used as a fixed effect in the wolf model and as an offset for black bear and moose

	Wolf (mixed logistic)		Black bear (mixed negative binomial)		Moose (mixed negative binomial)	
Covariates	**β**	**95% CI** [Lower : Upper]	**β**	**95% CI** [Lower : Upper]	**β**	**95% CI** [Lower : Upper]
Intercept	-0.17	[-2.09 : 1.29]	**-3.30**	**[-3.57 : -3.02]**	**-2.69**	**[-2.91 : -2.44]**
Age15	0.20	[-1.96 : 2.21]	0.05	[-0.19 : 0.37]	**0.27**	**[0.06 : 0.51]**
Age25	0.46	[-0.92 : 2.68]	**-0.41**	**[-0.73 : -0.17]**	0.12	[-0.20 : 0.35]
Age35	0.30	[-1.63 : 2.94]	**-0.85**	**[-1.19 : -0.44]**	**-0.74**	**[-1.06 : -0.40]**
Age45	-0.35	[-1.99 : 2.24]	**-1.40**	**[-1.82 : -0.98]**	**-1.26**	**[-21.72 : -0.95]**
Lateral cover	**-0.64**	**[-1.04 : -0.27]**	-0.08	[-0.19 : 0.02]	-0.05	[-0.14 : 0.07]
Slope	-0.12	[-0.40 : 0.10]	-0.01	[-0.07 : 0.09]	-0.004	[-0.08 : 0.06]
Log(Traffic+1)	**0.42**	**[0.10 : 1.18]**	**-0.16**	**[-0.33 : -0.06]**	0.003	[-0.100 : 0.110]
Herbaceous cover			0.01	[-0.12 : 0.08]		
Log(forage+1)					**0.27**	**[0.11 : 0.56]**
Log(forage+1)²					**-0.20**	**[-0.44 : -0.02]**
Wolf use			**0.17**	**[0.09 : 0.28]**	**0.09**	**[0.03 : 0.16]**
Black bear use	**0.37**	**[0.08 : 0.71]**			0.03	[-0.03 : 0.11]
Moose use	**0.43**	**[0.07 : 0.82]**	0.06	[-0.03 : 0.17]		
Mixed	0.23[a]	[-0.16 : 0.77]	0.02[b]	[-0.08 : 0.13]		
Coniferous	0.05[a]	[-0.42 : 0.72]	**0.20[b]**	**[0.02 : 0.38]**		
Wetlands	**0.53[a]**	**[0.17: 0.92]**	-0.07[b]	[-0.17 : 0.00]		
Distance to water	-0.001	[-0.35 : 0.45]	-0.01	[-0.09 : 0.11]		
Road density					-0.04[a]	[-0.12 : 0.04]
0-20 Clearcuts					**-0.17[a]**	**[-0.30 : -0.04]**
Effort	**0.33**	**[0.01 : 0.75]**				
Local density			-0.08	[-0.19 : 0.01]	**0.18**	**[0.07 : 0.27]**
PCNM	**-0.63**	**[-1.07 : -0.04]**	**-0.45**	**[-0.56 : -0.34]**	**0.32**	**[0.19 : 0.42]**

a: Calculated in a 500-m radius buffer

b: Calculated in a 250-m radius buffer

DISCUSSION

We showed that fine-scale characteristics of logging roads, that are typically not considered when studying the use of roads by large mammals, appeared to play an important role in explaining the use of road segments by wolves, black bears and moose. Large-scale variables that contextualized roads in their environment also contributed to the top-ranking models, suggesting that both intrinsic characteristics of linear features and the immediate environment in which they are built are predictors of their use by large mammals. However, testing the influence of some variables failed for caribou, as the number of caribou photos taken by our automated cameras was insufficient to conduct statistical analyses explaining the variation in caribou use of logging roads. Nevertheless, such a low number of events is in line with our predictions and suggests that caribou in our study area continued to avoid logging roads regardless of the state of vegetation regrowth. This result would be consistent with the widely demonstrated avoidance of linear features by caribou (James et Stuart-Smith, 2000 ; Leblond et al., 2011 ; Dussault et al., 2012 ; Mumma et al., 2019b).

Fine-scale characteristics of roads shape their use by large mammals

According to our predictions, wolves were more likely to use logging roads that facilitate movements: the probability of use of a road was lower when the density of lateral cover was high. This finding is consistent with studies conducted in western Canada on other types of linear features where wolves selected features with sparser vegetation and moved faster when using them (Dickie et al., 2017b, 2017a; Finnegan et al., 2018b). We also showed that roads with a higher traffic volume had a greater probability of use by wolves, a result that could also support our ease of movement hypothesis. A higher traffic volume could maintain roadways cleared of vegetation, facilitating predator movement and thus being more attractive for wolves. Indeed, we previously demonstrated that whenever a road was used once by humans during summer, there was never a growing stem in the middle of the it (St-Pierre et al., 2021) and other studies have also demonstrated that the use of linear features by vehicles can damage regrowth and prevent its establishment (Hornseth et al., 2018; Pigeon et al., 2016). Features used by humans were also shown to positively influence wolf use (Tattersall et al., 2020a).

We found no effect of the percentage of herbaceous cover on the use of roads by black bears, but found an effect of road age, thus partially supporting our increased forage accessibility hypothesis. The intensity of use of roads by black bears significantly decreased with road age compared to the levels of use of 0–10 year-old roads. We interpret this result as the slow replacement of early seral vegetation selected by black bears by less palatable or accessible plant species as roads age. Indeed, previous studies showed that roadways, roadsides (Bastille-Rousseau et al., 2011; Lesmerises et al., 2015) and other linear features (e.g. seismic lines; Finnegan et al., 2018a, 2019; MacDonald et al., 2020) are often colonised by early-seral vegetation such as forbs, graminoids and shrub species that are selected by black bears (Latham et al., 2011; Tigner et al., 2014). Contrary to wolves, the use of roads by black bears was negatively influenced by traffic volume. This could be explained by the suppression of vegetation on roadways linked to the passage of vehicles that would compact the soil and break young stems (Hornseth et al., 2018; Pigeon et al., 2016; St-Pierre et al., 2021), but it could also be explained by the disturbance associated with humans and vehicles (ATVs) as black bears can avoid human activity (Duquette et al., 2017; Muhly et al., 2011; Zeller et al., 2019).

The intensity of road use by moose was explained by road age but in a nonlinear way, with a higher intensity of use of 11–20 year-old roads compared to younger (0–10 years old) and older (30+ years old) road segments. This suggests that food accessibility could play a role in explaining variation in the intensity of use of road segments by moose, which is supported by the positive effect of the number of deciduous stems (forage availability covariate) on moose intensity of use that we also found. Moose are known to be associated with and benefit from regenerating disturbances where forage is abundant (Fisher and Wilkinson, 2005; Rempel et al., 1997; Toews et al., 2018). The higher use of 11–20 year-old roads compared to younger roads and the subsequent decrease in use of older roads appears supported by the transition between different stages of vegetation regeneration. Mumma et al. (2021) showed that moose tended to select 9–24 year-old cutblocks while avoiding 1–8 year-old and older (25–40 years old) cutblocks. In Québec, Potvin et al. (2005) showed that 10 year-old clearcuts offered better habitat conditions (browse availability, regeneration height, and lateral cover) for moose than immediately after harvest which also aligns with our explanation. As logging roads are built for timber extraction and are consequently mostly the same age as the surrounding clearcuts, it could be argued that moose used more 11–20 year-old roads not because of the road itself, but due to the presence of 11–20 year-old cuts in the surrounding. Although we included the proportion of 0–20 year-old clearcuts in our models as a covariate to control for its effect, we were not able to break down the clearcut age category into more precise subcategories (e.g. 0–10, 11–20) because of statistical constraints. Nevertheless, to our knowledge, our study is the first to directly link the intensity of use of naturally regenerating linear features by moose to an increased abundance of forage on roads (but see Tattersall et al., 2020a who found similar results, but in the case of actively restored linear features). This result confirms the concerns raised regarding the potential attractiveness of deciduous regrowth on linear features to moose (Finnegan et al., 2018a; MacDonald et al., 2020; St-Pierre et al., 2021).

We noted that the intensity of use of one species of large mammals was influenced by the use made by others, as we found positive correlations between the wolf and black bear use in both the wolf and bear models, and between wolves and moose in the moose and wolf models. Tattersall et al. (2020b) have previously reported empirical evidence of co-occurrence between wolves and bears on seismic lines (at the daily scale), while other studies suggested that wolves were using roads to increase their probability of encounter with prey (i.e. moose and caribou; Dickie et al., 2020; Latham et al., 2011; Whittington et al., 2011). However, some caution is needed when interpreting these results; we evaluated co-use of a road segment during an entire summer (early June to mid-September), i.e. at a temporal scale that prevents from inferring the predator hunting (and prey avoidance) strategies. While wolves and moose were both using road segments at the scale of an entire summer, we consider that moose could have avoided roads recently used by wolves at a finer temporal scale (temporal niche partitioning, *sensu* Frey et al., 2017; Latombe et al., 2014). Positive interactions could also have been a result of a shared use of roads with similar characteristics rather than species responding to each other (Tattersall et al., 2020b). Our results suggest that wolves, black bears and moose sometimes use logging roads with similar characteristics, meaning that road reclamation targeting one species could potentially influence the use and distribution of other sympatric mammals.

Large mammals respond to the landscape context surrounding logging roads

The probability of use of a road by wolves increased when the proportion of wetlands (peatlands, marsh) in the surrounding area was higher, which can be potentially explained by poor regrowth on such roads. In a companion study conducted on the same road segments, we showed that roads surrounded by a higher proportion of wetlands had a sparser lateral cover (i.e. a lower density of stems; St-Pierre et al. 2021). With our automated cameras, we showed that the probability of use of a road by wolves was higher when the density of lateral cover was low. Our result thus suggests that these poorly regenerated roads further facilitate wolf movements in wetlands and are thus more likely to be used by them; considering the selection of wetlands by caribou (Hins et al., 2009; James et al., 2004; Leblond et al., 2011; McLoughlin et al., 2005), we believe that these roads could increase the probability of encounter between wolves and caribou. Seismic lines located in lowlands were also shown to support poor regrowth in western Canada (Finnegan et al., 2019; Van Rensen et al., 2015), and wolves were shown to select linear features in peatlands (Mumma et al., 2019b). Such findings are of great concern considering that peatlands are often used as a spatial refuge for caribou, and the presence of roads in these habitats could increase wolf access to these refuges (DeMars and Boutin, 2018).

The use of logging roads by black bears was modulated by the composition of the surrounding environment; we showed that it was positively influenced by the surrounding proportion of coniferous stands, although a 95% confidence interval close to 0 (i.e. 0.02) suggests a weak effect. This result could be due to the feeding behavior of female black bears with cubs and their relative selection of coniferous stands. In their study, Lesmerises and St-Laurent (2017) showed that females with cubs selected old coniferous stands—which are considered to be of low food value—to avoid predation on cubs by big males who are more present in food-rich habitat such as clearcuts. Lesmerises et al. (2015) also showed that secondary roads provide important food sources (i.e. poplar and grasses) for female black bears with yearling cubs. In our case, females with cubs present in coniferous stands could have thus been using roads to forage, explaining higher use of roads surrounded by coniferous stands by black bears. We however point out that we did not consider sex in this study and that our interpretation should be considered with caution.

We showed that a higher proportion of clearcuts surrounding a road reduced its use by moose. When forage is abundant near a logging road, the potential benefit of food accessibility on the road is reduced, and moose could consequently use them less and spend more time foraging in adjacent cuts. This result may seem counterintuitive, as one could predict that moose would use roads to move faster between food-rich patches (clearcuts). However, moose are known to exhibit lower movement rates in food-rich areas (Dussault et al., 2005) and to select regenerating cutblocks where food availability is high (Dussault et al., 2006; Mumma et al., 2021) which support our results. Also, the selection of roads by wolves (Dickie et al., 2017a), the main predator of moose, could also discourage moose from using roads to facilitate its movements.

MANAGEMENT IMPLICATIONS

In her important report, Ray (2014) argued that vegetation on linear features will need to be both functionally and structurally restored for restoration of caribou habitat to have higher probabilities of being effective. Our study supports this conclusion, as we showed that both components need to be considered. While the functional role of roads (ease of movement) had an effect on wolf use, the structure and composition of regrowth positively influenced its use by black bears and moose. Based on our results, roads with no regrowth located in wetlands, which were more used by wolves, and roads with deciduous regrowth, attractive for bears and moose, should be prioritized for active restoration. Ray (2014) also suggested that restoration of caribou habitat needs to respond to the specific drivers of caribou decline operating in a given study area. For example, predation on caribou calves by black bears might be a more important limiting factor in some populations (i.e. Charlevoix; Leclerc et al. 2014), making the restoration of road segments suitable to black bears a priority in these populations, especially considering that the restoration of the entire derelict road network is impossible or logistically and financially too complex. We recognize that road decommissioning and habitat restoration cannot be the sole caribou conservation strategy to advocate as the small-scale restoration of suitable caribou habitat on linear features will be insufficient to reverse the decline of caribou populations. Nevertheless, we consider that such surgical prioritization based on road fine-scale characteristics could guide road decommissioning and habitat restoration and be an interesting approach when combined with other conservation strategies (e.g. protected areas, maternity penning, predator control; Dickie et al., 2021; Johnson et al., 2019; Serrouya et al., 2020).

One of the key findings regarding the role of linear features in caribou declines was that these structures increased encounter rates between wolves and caribou, resulting in a higher predation risk near these features (Whittington et al., 2011; Leblond et al., 2013; Mumma et al., 2017). It is thus necessary to determine whether the predation risk for caribou does increase near roads that have vegetation characteristics attractive to wolves, black bears, and moose or whether the increased use of roads by these large mammals does not translate into a lower caribou survival. Monitoring the success of restoration has already been conducted in the first years following restoration (Dickie et al., 2021; Lacerte et al., 2021; Tattersall et al., 2020a); however, doing so over a longer time period will further improve our comprehension and ability to effectively restore caribou habitat.

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APPENDIX.C. LIST OF CANDIDATE MODELS FOR EACH SPECIES AND ADDITIONAL INFORMATION ON COVARIATES, SAMPLED ROAD DISTRIBUTION AND EVENTS

Table C.1. List of candidates mixed logistic regression models used to model the probability of use of logging roads by wolves in boreal caribou range in Québec, Canada during three consecutive summers in 2018-2020. Covariates composing each model, their likelihood (LL) and relative support (ΔAIC_c) are shown. The effort and a PCNM as fixed effects and as a random effect at the road-year level were also included in each model

Model	**Explanatory covariates**	**LL**	**k**	ΔAIC_c
1 – Ease of travel	Age category + Slope + % of lateral cover	-349.69	5	0.83
2 – Co-use	log(Traffic volume+1) + Moose use + Wolf use	-356.11	5	7.51
3 – Road-scale	Model 1 + Model 2	-346.29	8	0.25
4 – Anthropogenic footprint	% of clear cuts + Road density	-362.89	4	19.01
5 – Habitat	% of mixed stands + % of coniferous stands + % wetlands + Distance_to_water	-356.77	6	10.87
6 – Surrounding environment-scale	Model 4 + Model 5	-356.52	8	12.43
7 – Ease of travel + Anthropogenic footprint	Model 1 + Model 4	-349.46	7	4.51
8 – Ease of travel + Habitat	Model 1 + Model 5	-345.96	9	1.69
9 – Co-use + Anth_Foot	Model 2 + Model 4	-356.08	7	11.54
10 – Co-use + Habitat	Model 2 + Model 5	-349.70	9	2.93
11 – Road-scale + Anth_Foot	Model 3 + Model 4	-345.95	10	3.77
12 – Road-scale + Habitat	Model 3 + Model 5	-341.96	12	0.00
13 – Environment-scale + Ease of travel	Model 6 + Model 1	-345.99	11	3.83
14 – Environment-scale + Co-use	Model 6 + Model 2	-349.62	11	4.83
15 – Full model	Model 3 + Model 6	-342.02	14	2.24

Table C.2. List of candidates mixed negative binomial regression models used to model the intensity of use of logging roads by black bears in boreal caribou range in Québec, Canada during three consecutive summers in 2018-2020. Covariates composing each model, their maximum likelihood (LL) and relative support (ΔAIC_c) are shown. The effort as an offset, a PCNM and black bear density as a fixed effect and as a random effect at the road-year level were also included in each model

Model	**Explanatory covariates**	**LL**	**k**	**ΔAIC_c**
1 – Forage accessibility	Age category + Slope + % of lateral cover + Mean herbaceous cover	-1266.87	4	9.72
2 – Co-use	log(Traffic volume+1) + Moose use + Wolf use	-1276.41	3	20.54
3 – Road-scale	Model 1 + Model 2	-1258.87	7	0.0
4 – Anthropogenic footprint	% of clear cuts + Road density	-1279.40	2	24.48
5 – Habitat	% of mixed stands + % of coniferous stands + % wetlands + Distance_to_water	-1281.51	4	32.79
6 – Surrounding environment-scale	Model 4 + Model 5	-1278.37	6	28.59
7 – Forage + Anthropogenic footprint	Model 1 + Model 4	-1266.67	6	13.51
8 – Forage + Habitat	Model 1 + Model 5	-1264.02	8	12.40
9 – Co-use + Anth_Foot	Model 2 + Model 4	-1270.12	5	12.08
10 – Co-use + Habitat	Model 2 + Model 5	-1271.93	7	19.85
11 – Road-scale + Anth_Foot	Model 3 + Model 4	-1258.79	9	4.05
12 – Road-scale + Habitat	Model 3 + Model 5	-1255.59	11	1.88
13 – Environment-scale + Forage	Model 6 + Model 1	-1264.92	10	16.30
14 – Environment-scale + Co-use	Model 6 + Model 2	-1268.77	9	15.61
15 – Full model	Model 3 + Model 6	-1256.76	13	6.35

Table C.3. List of candidates mixed negative binomial regression models used to model the intensity of use of logging roads by moose in boreal caribou range in Québec, Canada during three consecutive summers in 2018-2020. The covariates included in each model, their maximum likelihood (LL) and relative support (ΔAIC_c) are shown. The effort as an offset, a PCNM as a fixed effect as well as a random effect at the road-year level were also included in each model

Model	**Explanatory covariates**	**LL**	**k**	**ΔAIC_c**
1 – Forage accessibility	Age category + Slope + % of lateral cover + log(Forage availability+1)^2	-1627.13	5	6.18
2 – Co-use	log(Traffic volume+1) + Black bear use + Wolf use	-1658.15	3	66.13
3 – Road-scale	Model 1 + Model 2	-1622.82	8	3.85
4 – Anthropogenic footprint	% of clear cuts + Road density	-1665.16	2	70.09
5 – Habitat	% of mixed stands + % of coniferous stands + % wetlands + Distance_to_water	-1665.35	4	74.33
6 – Surrounding environment-scale	Model 4 + Model 5	-1662.60	6	70.90
7 – Forage + Anthropogenic footprint	Model 1 + Model 4	-1622.77	7	1.64
8 – Forage + Habitat	Model 1 + Model 5	-1623.37	9	7.05
9 – Co-use + Anth_Foot	Model 2 + Model 4	-1657.65	5	61.00
10 – Co-use + Habitat	Model 2 + Model 5	-1658.15	7	66.13
11 – Road-scale + Anth_Foot	Model 3 + Model 4	-1618.79	10	0.00
12 – Road-scale + Habitat	Model 3 + Model 5	-1619.40	12	5.48
13 – Environment-scale + Forage	Model 6 + Model 1	-1620.96	11	4.34
14 – Environment-scale + Co-use	Model 6 + Model 2	-1655.16	9	62.24
15 – Full model	Model 3 + Model 6	-1616.87	14	2.55

Table C.4. Covariates used in the mixed logistic regression models used to explain variations in the probability of use of logging roads by wolves across boreal caribou range in Québec, Canada

Covariate	**Description**	**Type and range**
Ease of travel		
Age category	Time since road construction	Categorical with 5 levels: 0-10 (Age5), 11-20 (Age15), 21-30 (Age25), 31-40 (Age35), 40+ (Age45) years old.
% of lateral cover	Mean percentage of lateral cover at 15 m in both direction parallel to the road	Continuous positive [0 : 100]
Slope	Slope at each camera station	Continuous positive [0.00 : 19.21]
Co-use		
Log(Traffic volume+1)	Number of human events/effort on a log-scale	Continuous positive [0.00 : 1.35]
Moose use	Number of moose events/effort	Continuous positive [0.00 : 0.38]
Black bear use	Number of black bears events/effort	Continuous positive [0.00 : 0.27]
Anthropogenic footprint		
% of 0-20 Clearcuts	Proportion of 0–20-year-old clearcuts (%) in a buffer of 500-m radius	Continuous [0 : 97.14]
Road density	Road density in a 500-m radius buffer (km/km²)	Continuous [0 : 5.10]
Habitat		
% of coniferous stands	Proportion of >20-year-old coniferous stands (%) in a buffer of 500-m radius	Continuous [0.00 : 99.99]
% of mixed stands	Proportion of >20-year-old deciduous stands (%) in a buffer of 500-m radius	Continuous [0.00 : 63.48]
% of wetlands	Proportion of wetlands (%) in a buffer of 500-m radius	Continuous [0 : 14.83]
Distance towater	Distance to the nearest permanent water body (m)	Continuous [4.79 : 1126.66]
All model		
Effort	Days during which the camera was active	Continuous [10.02 : 120.03]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.04 : 0.04]
(1|RoadIDYear)	Random effect at the road-year level	Categorical with 165 levels

Table C.5. List of covariates used in the mixed negative binomial regression models used to explain variations in the intensity of use of logging roads by black bears across boreal caribou range in Québec, Canada

Covariate	Description	Type and range
Food accessibility		
Age category	Time since road construction	Categorical with 5 levels: 0-10 (Age5), 11-20 (Age15), 21-30 (Age25), 31-40 (Age35), 40+ (Age45) years old.
% of lateral cover	Mean percentage of lateral cover at 15 m in both direction parallel to the road	Continuous positive [0 : 100]
Slope	Slope at each camera station	Continuous positive [0.00 : 19.21]
Herbaceous cover	Relative mean herbaceous cover (%)	Continuous positive [0.00 : 90.00]
Co-use		
Log(Trafficvolume+1)	Number of human events/effort on a log-scale	Continuous positive [0.00 : 1.35]
Moose use	Number of moose events/effort	Continuous positive [0.00 : 0.38]
Wolf use	Number of wolf events/effort	Continuous positive [0.00 : 0.25]
Anthropogenic footprint		
% of 0-20 Clearcuts	% of 0–20-year-old clearcuts in a buffer of 250-m radius	Continuous [0 : 99.99]
Road density	Road density in a 250-m radius buffer (km/km²)	Continuous [0 : 8.03]
Habitat		
% of coniferous stands	% of >20-year-old coniferous stands in a buffer of 250-m radius	Continuous [0.00 : 99.99]
% of mixed stands	% of >20-year-old deciduous stands in a buffer of 250-m radius	Continuous [0.00 : 85.73]
% of wetlands	% of wetlands in a buffer of 250-m radius	Continuous [0 : 23.96]
Distance to water	Distance to the nearest permanent water body (m)	Continuous [4.79 : 1126.66]
All model		
Effort	Days during which the camera was active.	Offset [10.02 : 120.03]
Regional density	Estimated density of black bears per region per year (bear/km²)	Continuous [0.02 : 0.09]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.04 : 0.04]
(1|RoadIDYear)	Random effect at the road-year level	Categorical with 165 levels

Table C.6. Covariates used in the mixed negative binomial regression models used to explain variations in the intensity of use of logging roads by moose across boreal caribou range in Québec, Canada

Covariate	**Description**	**Type and range**
Food accessibility		
Age category	Time since road construction	Categorical with 5 levels: 0-10 (Age5), 11-20 (Age15), 21-30 (Age25), 31-40 (Age35), 40+ (Age45) years old.
% of lateral cover	Mean percentage of lateral cover at 15 m in both direction parallel to the road	Continuous positive [0 : 100]
Slope	Slope at each camera station	Continuous positive [0.00 :1 9.21]
Forage availability	Sum of white birch, willows and trembling aspen stems in a 32 m² surface	Discrete positive [0 : 57]
Co-use		
Log(Traffic volume+1)	Number of human events/effort on a log-scale	Continuous positive [0.00 : 1.35]
Black bear use	Number of black bear events/effort	Continuous positive [0.00 : 0.27]
Wolf use	Number of wolf events/effort	Continuous positive [0.00 : 0.25]
Anthropogenic footprint		
% of 0-20 Clearcuts	Proportion of 0–20-year-old clearcuts (%) in a buffer of 250-m radius	Continuous [0 : 99.99]
Road density	Road density in a 250-m radius buffer (km/km²)	Continuous [0 : 8.03]
Habitat		
% of coniferous stands	% of >20-year-old coniferous stands in a buffer of 250-m radius	Continuous [0.00 : 99.99]
% of mixed stands	% of >20-year-old deciduous stands in a buffer of 250-m radius	Continuous [0.00 : 85.73]
% of wetlands	% of wetlands in a buffer of 250-m radius	Continuous [0 : 23.96]
Distance to water	Distance to the nearest permanent water body (m)	Continuous [4.79 : 1126.66]
All model		
Effort	Days during which the camera was active.	Offset [10.02 : 120.03]
Regional density	Estimated density of moose per region per year (moose/km²)	Continuous [0.20 : 0.94]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.04 : 0.04]
(1|RoadID-Year)	Random effect at the road-year level	Categorical with 165 levels

Table C.7. Raw and standardized (per 10,000 camera-days) number of events (i.e. number of photographed animals) captured by cameras placed on logging roads and in adjacent forest during three consecutive summers of 2018-2020 in boreal caribou range in Québec, Canada

Species	Raw events on roads	Raw events in adjacent forest	Events on roads per 10,000	Events in forest per 10,000
Moose	3614	277	622	93
Black bear	1866	115	321	38
Grey wolf	1125	6	194	2
Caribou	36	9	6	3

Table C.8. Breakdown of sampled logging road segments into age categories (no. of years since construction) and regions (CN: Côte-Nord, LSJ: Saguenay-Lac-St-Jean, LWR: Laurentides Wildlife Reserve) across boreal caribou range in Québec, Canada

Region	Age category					
	0-10	**11-20**	**21-30**	**31-40**	**40+**	**Total**
CN	2	4	4	0	5	15
LSJ	1	1	3	7	3	15
LWR	3	2	6	6	9	26
Total	6	7	13	13	17	56

APPENDIX D. METHOD USED TO CALCULATE THE DETECTION ZONES OF RANDOM CAMERAS

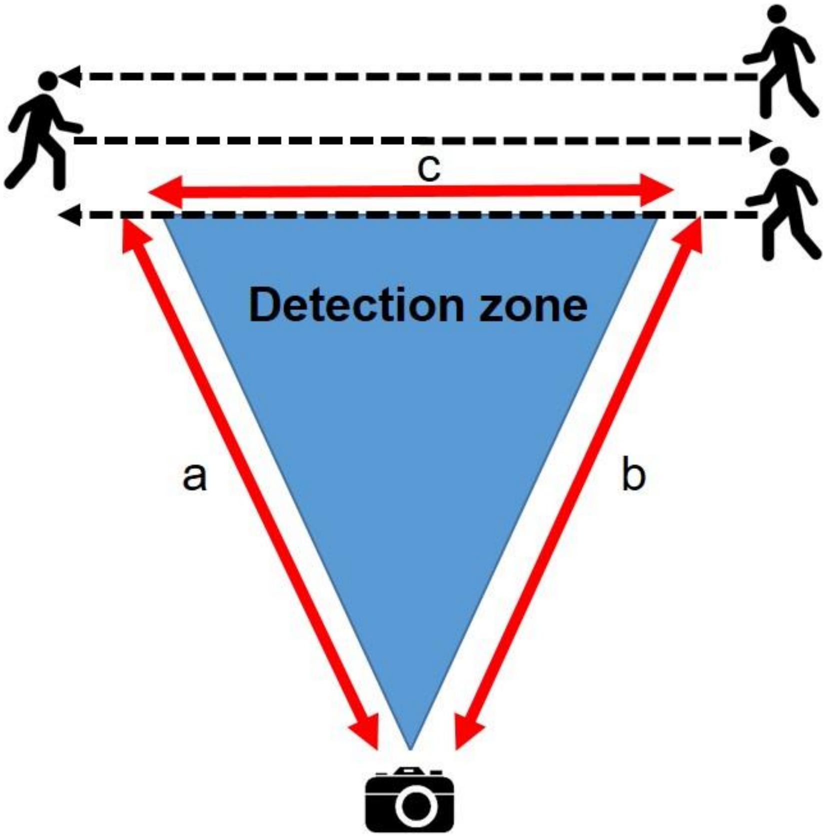

Figure D.1. Visual representation of the method used to determine the detection zone. A series of passages were made starting further away and gradually closer to the camera until it detected movement. We then noted the length of each sides (letter a, b and c) of the detection zone to later derivate the detection angle and area.

We made a series of passages in front of each adjacent forest camera to determine the length of the sides of the detection zone. The first passage was done further away from the camera, where we knew it would not detect any movement, and each subsequent passage was done gradually closer to the camera until we were certain the camera detected it. We then measured the length of each side: a (distance from the camera to the leftmost detected movement), b (distance from the camera to the rightmost detected movement) and c (distance between leftmost detection and rightmost detection). We used these measurements to calculate the detection zone and the detection angle (angle ab).

CONCLUSION GÉNÉRALE

Objectifs

L'objectif de ce mémoire était de caractériser la régénération naturelle des chemins forestiers et d'identifier comment les différentes caractéristiques de ceux-ci influencent leur utilisation par les espèces de grands mammifères impliquées dans le déclin du caribou forestier (*Rangifer tarandus caribou*). Cet objectif était subdivisé en deux sous-objectifs qui ont fait l'objet des deux chapitres principaux de ce mémoire, soit 1) d'identifier les facteurs qui empêchent l'établissement de la régénération et qui en influencent la composition lorsqu'elle est présente, et 2) de déterminer comment les caractéristiques des chemins influencent leur utilisation par le caribou, l'orignal (*Alces americanus*), l'ours noir (*Ursus americanus*) et le loup gris (*Canis lupus*).

Retour sur les principaux résultats

Régénération naturelle des chemins forestiers

Les résultats du premier chapitre ont montré que des facteurs opérant à la fois à petite, moyenne et grande échelles influençaient la composition en essence de la régénération. La majeure partie de la variation de la composition était expliquée par un gradient du nombre de degrés-jours disponibles à la croissance et de proportions de forêts de conifères autour du tronçon de chemin étudié. La régénération était davantage composée d'épinette noire (*Picea mariana*) et de sapin baumier (*Abies balsamea*) lorsque les chemins étaient plus âgés, entourés d'une plus grande proportion de forêt de conifères et situés dans des régions recevant un plus faible nombre de degrés-jours de croissance. À l'inverse, les chemins plus jeunes, entourés d'une plus faible proportion de forêts résineuses et situés dans des régions où le nombre de degrés-jour de croissance est plus élevé supportaient une régénération dominée par l'aulne (*Alnus spp*.). Un sol plus compacté semblait aussi favoriser l'aulne. Nos résultats montrent que la régénération des chemins forestiers peut suivre différentes trajectoires de succession forestière, en étant composée soit d'essences feuillues tolérantes aux perturbations ou, sous d'autres conditions, d'essences résineuses représentatives de des peuplements non-perturbés à proximité du chemin. De plus, près du quart (22 %) des parcelles étudiées n'avait pas été recolonisées passivement par de la végétation et demeuraient ainsi dans un état perturbé. Ces résultats concordent avec ceux obtenus dans l'étude du potentiel de régénération passif de lignes d'exploration sismique qui ont elles aussi montré un faible degré de régénération naturelle qui était souvent dominée par des essences feuillues tolérantes aux perturbations (Lee et Boutin, 2006 ; Finnegan et coll., 2018a).

Nos résultats montrent que la compaction était le principal facteur qui empêchait l'établissement de la régénération dans l'assise des chemins forestiers. Cette variable était reliée à une plus faible densité de couvert latéral et à une plus faible probabilité de compter au moins une tige >1,30 m au centre du chemin. Bien que les effets négatifs de la compaction des sols sur la croissance racinaire et conséquemment sur le développement des plantes étaient jusque-là bien documentés en sol forestier (p. ex. Cambi et coll., 2015), notre étude est la première à directement relier la compaction à la régénération naturelle des chemins forestiers dans l'habitat du caribou. L'utilisation des chemins par les villégiateurs avait aussi un effet négatif important sur l'établissement de la régénération, puisqu'aucune tige ne poussait au centre des chemins lorsque ceux-ci étaient utilisés au moins une fois par les villégiateurs pendant un été, possiblement en raison des dommages occasionnés à la régénération ou au maintien des sols compactés par les véhicules (Pigeon et coll., 2016 ; Hornseth et coll., 2018). Finalement, la densité du couvert latéral était plus faible dans les chemins ceinturés d'une plus grande proportion de milieux humides, potentiellement en lien avec la banque de graine aérienne majoritairement composée d'épinettes noires et de mélèzes (*Laryx laricina*) et la piètre qualité du substrat des chemins forestiers comme lit de germination pour ces essences.

Utilisation des chemins forestiers par les grands mammifères

Les résultats du deuxième chapitre ont montré quant à eux l'importance des caractéristiques individuelles des chemins sur leur utilisation par le loup, l'ours noir et l'orignal. L'état de la régénération des chemins influençait de manière différente leur utilisation. La structure de la régénération dans l'assise d'un chemin semblait davantage influencer son utilisation par le loup. En effet, la probabilité d'occurrence du loup était plus importante lorsque la végétation sur les chemins offrait une plus faible densité de couvert latéral. De tels chemins avec une régénération éparse sont reconnus pour faciliter les déplacements dans le paysage et sont alors conséquemment favorisés par les prédateurs (Dickie et coll., 2017 ; Finnegan et coll., 2018b). L'utilisation des chemins par l'ours noir et l'orignal semblait quant à elle davantage reliée à l'accès à de la nourriture digestible et palatable. En effet, nos résultats montrent que ces deux espèces utilisaient davantage les chemins plus jeunes comparativement à ceux plus âgés, possiblement en raison de la régénération d'espèces pionnières feuillues qui représente une source de nourriture importante pour ces deux mammifères (Potvin et coll., 2005 ; Lesmerises et coll., 2015). De plus, l'utilisation des chemins par l'orignal était positivement reliée au nombre de tiges d'essences ligneuses feuillues (peuplier faux-tremble *Populus tremuloides*, bouleau à papier *Betula papyrifera* et saules *Salix spp*.) poussant sur l'assise des chemins, soulignant l'importance de la composition de la régénération pour cette espèce.

Le contexte spatial dans lequel un chemin est situé jouait aussi un rôle dans le niveau d'utilisation exercée par les grands mammifères. En effet, la probabilité qu'un chemin soit utilisé par le loup était plus importante lorsque celui-ci était entouré d'une proportion plus élevée de milieux humides. De plus, les chemins entourés d'une plus grande proportion de forêts de conifères étaient davantage utilisés par l'ours noir alors que ceux avec une plus faible proportion de jeunes coupes (0-20 ans) étaient davantage utilisés par l'orignal.

Contributions appliquées à la conservation du caribou forestier

La protection et le rétablissement des populations boréales du caribou des bois (aussi appelées « caribou forestier » au Québec) représentent peut-être l'un des plus grands défis de conservation auquel le Canada fait face (Hebblewhite, 2017 ; Johnson et coll., 2019 ; Serrouya et coll., 2019). Bien que le problème des structures anthropiques linéaires et la nécessité de les remettre en production soient de plus en plus reconnus, aucune étude n'avait jusqu'ici caractérisé la composition en essence et les facteurs empêchant la régénération naturelle des chemins forestiers. Nos résultats offrent la première description de la régénération naturelle des chemins forestiers dans l'habitat du caribou au Canada et soulignent l'importance d'entreprendre des mesures de démantèlement actives des chemins. En effet, nous avons montré que la remise en production passive (c.-à-d. laisser les chemins se régénérer de façon naturelle) est lente et n'est pas toujours garante de succès. Les résultats du chapitre 1 ont d'ailleurs montré que l'âge n'est pas un bon prédicteur de l'état de la régénération d'un chemin. Ce résultat est important, car avant notre projet l'âge était souvent identifié comme un des critères principaux de priorisation pour la restauration. Notre projet a d'ailleurs été mis sur pied dans la foulée d'une question transmise à notre équipe de recherche par les autorités du Ministère des Forêts, de la Faune et des Parcs du Québec ; existe-t-il un âge à partir duquel les chemins forestiers peuvent être considérés comme suffisamment régénérés pour ne plus représenter une perturbation défavorable au caribou et, par conséquent, ne pas nécessiter d'efforts actifs de remise en production ? En réponse à ce questionnement, nos résultats montrent que les caractéristiques propres à chaque chemin (p. ex. la structure et la composition de la régénération) ainsi que leur contexte spatial (p. ex. type de peuplement à proximité) devraient plutôt être utilisées pour identifier les chemins à prioriser pour des travaux de démantèlement à l'échelle de l'aire de répartition du caribou forestier.

En mettant en lumière la relation entre les caractéristiques individuelles des chemins et leur utilisation à la fois par le loup, l'ours noir et l'orignal, nos résultats permettront d'adapter le démantèlement des chemins forestiers aux moteurs de déclin spécifiques à chaque population de caribou, tel que suggéré par Ray (2014). Par exemple, dans le cas d'une population où la prédation par l'ours noir représente le principal facteur limitant la survie (p. ex. Charlevoix, Leclerc et coll., 2014), le démantèlement pourrait prioriser les jeunes tronçons de chemin supportant une régénération feuillue considérant que sur la base de nos résultats, ces derniers étaient davantage utilisés par l'ours. À l'inverse, dans le cas d'une population dont la persistance est limitée par la prédation exercée par le loup (p. ex. Chinchaga, Johnson et coll., 2019), le démantèlement pourrait prioriser les chemins ceinturés d'une plus grande proportion de milieux humides et avec une plus faible densité de couvert latéral sans égard à l'âge (qui s'avérait être un mauvais prédicteur de l'utilisation faite par le loup). Ajuster ainsi les efforts de restauration de l'habitat aux moteurs de déclin propres à chaque population devrait permettre de maximiser l'efficacité de telles mesures au bénéfice du rétablissement du caribou.

Finalement, nos résultats ont d'importantes implications relatives aux méthodes de démantèlement des chemins à préconiser. Comme la compaction représentait la principale variable qui empêchait l'établissement et la croissance de la régénération, la décompaction de l'assise des chemins avec de la machinerie apparaît être une étape nécessaire des efforts de démantèlement actif, un résultat récemment confirmé par Lacerte et coll. (2021). Restreindre l'accès des villégiateurs aux tronçons récemment restaurés s'avère aussi être une mesure importante à mettre en place considérant les effets négatifs du passage de véhicules sur la régénération que nous avons mis en lumière (voir le chapitre 1) et la relation positive entre l'utilisation des villégiateurs et celle du loup (soulignée au chapitre 2). En considérant le rôle important des peuplements résineux matures à proximité dans l'établissement d'une régénération naturelle résineuse, la plantation de semis s'avère aussi essentielle lorsqu'un chemin restauré se trouve en paysage hautement perturbé (p. ex. coupe forestière) où très peu de peuplements adultes potentiellement semenciers sont observés à proximité du chemin.

Contributions théoriques

D’un point de vue plus fondamental, notre étude illustre comment les activités anthropiques peuvent avoir des effets sur les processus de succession végétale. Nos résultats montrent comment la modification de certains paramètres (p. ex. paramètres physique : compaction du sol) contribuent à modifier la trajectoire de succession végétale vers un état alternatif de succession. Notre étude contribue à mieux comprendre comment les perturbations anthropiques ont le potentiel de modifier le jeu spatial prédateurs-proies dans un système où plusieurs prédateurs et plusieurs proies coexistent (Lima, 2002). En effet, nos résultats montrent que le loup, l’ours et l’orignal peuvent utiliser les mêmes chemins forestiers pendant un été, ce qui a potentiellement des implications sur les taux de rencontres prédateurs-proies. Les résultats du chapitre 2 ont montré que la réponse de deux prédateurs aux perturbations anthropiques n’est pas la même en fonction des caractéristiques de ces perturbations, un résultat appuy. Par Leblond et coll. (2016). Finalement, notre étude souligne l’utilité des caméras à détection automatique dans l’étude des interactions entre les espèces fauniques et les perturbations anthropiques, un champ d’études émergeant (Smith et coll., 2020).

Limites

Bien qu’apportant des éléments novateurs, notre étude comporte certaines limites. Tout d’abord, les résultats du chapitre 1 se concentrent principalement sur la composition et l’établissement de la régénération arbustive et arborescente des chemins, car les mesures utilisées pour les analyses considéraient uniquement les tiges présentant un diamètre à hauteur de poitrine mesurable (c.-à-d. à ~1,30 m du sol, ce qui exclut les tiges d’une hauteur inférieure à 1,30 m). De plus, caractériser la composition et les facteurs influençant la régénération herbacée sur les assises de chemins forestiers pourrait être également très informatif considérant l’importance de certaines plantes herbacées dans le régime alimentaire de l’ours noir (Lesmerises et coll., 2015) et de l’orignal (Hodder et coll., 2013).

Dans cette étude, nous nous sommes concentrés sur la régénération présente directement sur l’assise des chemins. Toutefois, nous reconnaissons que l’influence des perturbations anthropiques linéaires sur la composition de la régénération peut s’étendre en bordure de l’assise, dans l’emprise de part et d’autre de la surface de roulement (Finnegan et coll., 2018a ; MacDonald et coll., 2020, Dabros et coll., 2021). De plus, peu d’information était disponible quant aux méthodes de construction des chemins qui auraient pu évoluer au fil des années ou être différentes en fonction des conditions du terrain (p. ex. milieu humide, pente forte) et avoir par conséquent un impact sur la régénération.

Finalement, nous sommes conscients que les résultats du chapitre 2, qui porte sur l’utilisation des chemins forestiers par les grands mammifères, sont essentiellement corrélatifs, bien qu’appuyés par une littérature empirique abondante détaillant les différentes parties du mécanisme reliant les structures linéaires au déclin du caribou (Whittington et coll., 2011 ; Leblond et coll., 2013 ; Mumma et coll., 2018). Par conséquent, nos conclusions dépendent du respect de la prémisse voulant qu’une plus grande utilisation des chemins présentant certaines caractéristiques favorables par le loup, l’ours noir et l’orignal puisse se traduire par un plus grand risque de rencontre et de prédation sur le caribou près de ces structures. Sur la base des connaissances disponibles à ce jour, nous sommes néanmoins confiants quant à la portée de nos conclusions.

Conclusion et orientations futures en recherche

Dans un contexte où la demande en ressources naturelles ne cesse d’augmenter, la compréhension des effets des perturbations anthropiques est essentielle afin de limiter les impacts du développement humain sur la biodiversité et ainsi améliorer nos stratégies de conservation (Gauthier et coll., 2015 ; Anderman et coll., 2020). Les chemins forestiers représentent une forme majeure de perturbation en forêt boréale et ont des effets négatifs qui vont bien au-delà du cas spécifique du caribou forestier (voir Daigle, 2010 ainsi que Robinson et coll., 2010 et St-Laurent et coll., 2012 pour des revues de littérature sur l’effet des chemins en milieux forestiers). Bien que notre étude se soit concentrée sur le caribou, elle offre une compréhension plus générale des déterminants de la régénération forestière et, par le fait même, de la persistance des chemins forestiers, et pourra ainsi contribuer à la conservation d'autres espèces tout autant affectées par les perturbations anthropiques linéaires retrouvées en forêt boréale (p. ex. carcajou *Gulo gulo* : Kortello et coll., 2019).

Dix années se sont maintenant écoulées depuis l'étude pionnière de Whittington et coll. (2011) qui avait souligné le rôle des perturbations anthropiques linéaires dans l'augmentation du taux de rencontre entre le caribou et le loup. Plusieurs études ont depuis été conduites et ont amélioré notre compréhension du lien entre ce type de perturbation et le déclin du caribou forestier (p. ex. Leblond et coll., 2013 ; Dickie et coll., 2017; Mumma et coll., 2017, 2018). Notre étude s'ajoute à cet important effort de recherche et comble en partie l'écart de connaissances observé entre les lignes d'exploration sismiques dans l'ouest du pays relativement au cas spécifique des chemins forestiers qui constituent la perturbation linéaire la plus commune dans l'est du Canada. De futures études qui analyseront l'efficacité à long terme des efforts de remise en production (tant actif que passif) des structures anthropiques linéaires sur l'établissement de la régénération, mais aussi sur leur utilisation par les grands mammifères, nous permettrons d'améliorer d'autant plus nos interventions, le tout au bénéfice du caribou forestier.

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