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Avant-propos

Le présent mémoire de maîtrise est composé de trois chapitres. Le premier chapitre comprend l'introduction générale du mémoire, décrivant la problématique et les objectifs. Le deuxième chapitre, rédigé en anglais, présente l'article scientifique qui sera soumis dans les prochains mois à la revue scientifique *Forest Ecology and Management*. Le co-directeur, M. Louis Imbeau, est le deuxième auteur et le directeur, M. Marc J. Mazerolle, est le dernier auteur. L'auteur principal des trois chapitres est la candidate à la maîtrise en sciences forestières, Mathilde Lapointe St-Pierre. Le troisième chapitre est une conclusion générale, rédigée en français.

Ce projet de maîtrise représente un grand travail d'équipe, c'est pourquoi je tiens à remercier premièrement mes directeurs, Marc J. Mazerolle et Louis Imbeau. Merci pour votre bon encadrement et votre intégrité scientifique. Merci à Louis pour ta bonne humeur et tes commentaires positifs. Merci à Marc d'avoir partagé avec moi ta passion des amphibiens et des reptiles. Tes connaissances, ta rigueur ainsi que tes grandes disponibilités m'ont grandement aidé à cheminer dans ce projet. Grace à toi, j'ai développé des habilités en analyses statistiques ainsi qu'en recherche scientifique. Merci de m'avoir fait confiance pour ce projet!

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"Debugging is twice as hard as writing the code in the first place. Therefore, if you write the code as cleverly as possible, you are, by definition not smart enough to debug it."

\- *Brian Kernighan*

Chapitre 1. Introduction générale

Les défis de l'implantation de l'aménagement écosystémique en forêts mixtes et feuillues

Depuis plus d'un siècle, l'exploitation forestière a grandement modifié le paysage forestier québécois en diminuant la proportion des vieilles forêts (Bouchard et Pothier, 2011), en simplifiant la structure des peuplements, et en réduisant la quantité de bois mort retrouvée au sol (Boucher *et al.*, 2009; Boucher et Grondin, 2012). Afin d'assurer une récolte forestière durable et de limiter les impacts potentiels sur la biodiversité, le Québec s'est récemment tourné vers l'aménagement écosystémique (Gauthier *et al.*, 2008). Ce principe vise de façon générale à ce que l'aménagement des forêts soit adapté au régime de perturbations naturelles d'une région donnée. Ainsi, les traitements forestiers basés sur l'aménagement écosystémique devraient respecter les limites de la variabilité naturelle observées à l'échelle d'un peuplement (Raymond *et al.*, 2009). En diminuant l'écart entre les forêts naturelles et aménagées, ces pratiques favorisent la viabilité des processus écologiques et le maintien de la diversité biologique. Puisqu'il s'agit d'une approche adaptative qui évolue en fonction des innovations scientifiques, de nouvelles méthodes sont continuellement mises en place afin d'assurer la résilience des forêts aménagées (Gauthier *et al.*, 2008).

Plusieurs perturbations naturelles sont retrouvées au Québec et créent des peuplements à structure équienne ou inéquienne, selon leur intensité (Gauthier *et al.,* 2008). C'est particulièrement le cas des forêts mixtes et feuillues, où les principales perturbations sont à petite échelle et sont générées par une dynamique de trouées (Lorimer et Frelich, 1994). Il en résulte des peuplements inéquiens. Grâce à leur structure qui miment l'impact des trouées, les coupes progressives irrégulières (CPI) seraient aptes à maintenir la diversité biologique et la viabilité des écosystèmes et s'intègreraient bien au paysage forestier des forêts mixtes (Raymond *et al.*, 2009). En effet, ce type de traitement est classé dans le régime de la futaie irrégulière et découle du Femelschlag. Cette pratique sylvicole est une des premières méthodes d'exploitation irrégulière et est utilisée en Europe depuis le début du 19^{e} siècle. Le Femelshlag est caractérisé par des coupes répétitives qui ont comme but de favoriser la régénération d'espèces mixtes (Schütz, 2002). Plusieurs traitements sylvicoles découlent du Femelschlag et diffèrent d'un pays à l'autre (Larouche *et al.*, 2013). Au Québec, les CPI ont généralement comme objectif de créer une régénération non-homogène (Lussier et Meek, 2014), par une série de coupes partielles, produisant ainsi un peuplement de 2 à

4 classes d'âges (Schütz, 2002; Raymond *et al.*, 2009; Kelen et Lessard, 2004). Il existe deux types de CPI : la CPI à couvert permanent qui vise le maintien d'un couvert d'arbres matures en permanence et la CPI à régénération lente, qui est composée de plusieurs coupes successives. Elles permettent la culture d'essences à tolérances et longévités variables (Joanisse *et al.*, 2014) et prennent forme selon trois principaux patrons de récoltes: par trouées agrandies, à couvert permanent et à régénération lente. Ces types de coupes répondent à des enjeux de peuplements différents. Elles ont un objectif commun qui est d'étaler la régénération sur une longue période de temps comparativement aux coupes du régime de futaie régulier (Raymond *et al.*, 2009).

Bien que les coupes progressives irrégulières aient fait leur apparition au Québec à la fin des années 1990, ce n'est que récemment que la commission d'étude sur la gestion de la forêt publique québécoise a popularisé ces pratiques en recommandant la CPI pour maintenir la structure irrégulière des peuplements (Poulin, 2013). Cependant, peu d'études ont évalué les conséquences des CPI sur l'environnement, ce qui soulève plusieurs questions quant aux effets de ces pratiques sur la faune. Afin d'approfondir les connaissances sur les CPI au Québec, il est nécessaire d'effectuer une étude de leur impact sur la diversité écologique. Dans le cadre de ce mémoire, nous nous attarderons plus particulièrement dans le cadre de ce travail sur les amphibiens, qui sont les vertébrés plus sensibles aux modifications mineures de microhabitat à l'échelle du peuplement.

Importance des amphibiens dans les écosystèmes forestiers

Depuis une vingtaine d'années, les scientifiques s'entendent sur un déclin alarmant des amphibiens, et ce, à l'échelle planétaire (Alford et Richards, 1999; Adam *et al.*, 2013; Böhm *et al.*, 2013). Chez les amphibiens, 187 espèces sont menacées par la perte et la dégradation de leur habitat (Stuart *et al.*, 2004). La dynamique des populations d'amphibiens est la première touchée par les perturbations des coupes forestières, puisque celles-ci perturbent à la fois le microclimat et le microhabitat (Ash, 1995; Demaynadier et Hunter, 1995; O'Donnell *et al.*, 2014). Cette sensibilité se traduit par un changement dans le statut de certaines populations. À ce titre, les amphibiens et les reptiles constituent une plus grande proportion d'espèces vulnérables et à risque de disparaître que les mammifères et les oiseaux (Gibbons *et al.*, 2000; Houlahan *et al.*, 2000; Stuart *et al.*, 2004). Au Canada, 42% des amphibiens sont désignés à risque par le COSEPAC et la plus grande menace est la perte et la dégradation de leurs habitats (Lesbarrères *et al.*, 2014).

Parmi les amphibiens, les salamandres terrestres occupent un rôle clé dans l'écosystème forestier. Les salamandres terrestres sont les plus importants prédateurs de la chaîne alimentaire des détritivores (Burton et Likens, 1975; Hairston, 1987) et sont également des proies de prédilection pour plusieurs espèces animales (Pough *et al.*, 1987). La salamandre cendrée (*Plethodon cinereus*) est le vertébré le plus abondant dans plusieurs forêts de l'est de l'Amérique du Nord (Burton and Likens, 1975; Petranka *et al.*, 1994; Milanovich et Peterman, 2016). Étant un animal fouisseur, elle a un impact positif sur la qualité des sols forestiers en modifiant la composition de la litière du sol et son taux de décomposition (Wyman, 1998; Davic et Welsh, 2004). La salamandre cendrée est la seule espèce d'amphibien au Québec à avoir un cycle complètement terrestre. Les juvéniles deviennent matures sexuellement 2 ans après l'éclosion (Saylor, 1966) et les femelles ont leur première ponte vers l'âge de 3,5 ans (Petranka, 1998). N'ayant pas besoin des habitats aquatiques pour se reproduire, elle a un comportement philopatrique et son domaine vital est restreint (Yurewicz et Wilbur, 2004). Les densités de salamandres cendrées varient entre 0,25 salamandre/m^2 (Burton et Likens, 1975) à 2,8 salamandres/m^2 (Matis, 1991) selon les régions dans lesquelles elles sont étudiées. Dépourvues de poumons, les salamandres du genre pléthodontidés dépendent d'un environnement humide qui permet les échanges gazeux nécessaires à la respiration cutanée (Heatwole et Lim, 1961). Elles se retrouvent à la surface du sol forestier lorsque la température et l'humidité sont idéales pour leur permettre de respirer, autrement elles effectuent des migrations verticales plus profondément dans le sol. Elles peuvent migrer verticalement durant de longues périodes, jusqu'à 90 cm de profondeur (Grizzell, 1949; Taub, 1961). Plus l'été devient chaud et sec, plus il est difficile d'observer cette espèce à la surface du sol (Fraser 1976; Jaeger 1980). Ces caractéristiques biologiques et restrictions physiologiques font de la salamandre cendrée un indicateur écologique pertinent pour suivre les changements d'un écosystème (Feder, 1983; Vitt *et al.*, 1990; Welsh et Droege, 2001).

Effets des pratiques sylvicoles sur les populations d'amphibiens

Petranka *et al.* (1994) et Pough *et al.* (1987) ont montré que les salamandres sont adaptées aux conditions environnementales des vieilles forêts matures et que les coupes forestières peuvent affecter leur abondance. À court terme, les coupes totales ont un impact rapide et négatif sur les populations de salamandres (Demaynadier et Hunter, 1995; Morneault *et al.*, 2004; Tilghman *et al.*, 2012). Petranka *et al.* (1993) a d'ailleurs déterminé que 75% à 80% des populations de salamandres disparaissent après des coupes totales dans les forêts appalachiennes de la Caroline du Nord. Bien que les coupes totales soient négatives pour les populations de salamandres, il n'y a pas de consensus à propos du temps minimum pour le retour des populations de salamandres après des perturbations forestières (résilience). Ash (1997) a observé que les populations de salamandres terrestres se rétablissent en quelques années. En effet, les populations de certaines espèces (*Plethodon jordani*) peuvent se rétablir en 2 ans seulement (Ash, 1988). En contrepartie, Hocking *et al.* (2012) rapportent qu'après 7 ans, il existe encore un impact négatif des coupes forestières sur les populations de salamandres terrestres. D'autres études évaluent que 20 à 80 ans sont nécessaires au rétablissement des salamandres terrestres (Petranka *et al*., 1993, 1994; Rota *et al.*, 2017 ; Homyack et Haas, 2009). Homyack *et al.* (2011), par exemple, ont trouvé un impact négatif de certaines coupes partielles, approximativement 10 années suivant la coupe, en étudiant la condition corporelle et le budget énergétique des salamandres.

D'autres études montrent que les coupes partielles n'ont pas ou peu d'effets sur les salamandres. Moore *et al.* (2002) n'ont pas détecté d'effet sur l'abondance des salamandres terrestres des coupes sélectives après 6 et 8 ans, ni des coupes totales après 12 ans. Rota *et al.* (2017) ont suivi pendant 23 ans l'impact de plusieurs types de coupes forestières sur différentes espèces d'amphibiens et de reptiles et ils n'ont pas trouvé d'impact des coupes forestières sur la majorité des espèces. Dans leur étude Knapp et al. (2003) n'ont relevé aucun impact négatif des coupes totales, des coupes progressives régulières et des coupes de jardinage sur l'abondance de salamandres terrestres. Ces derniers proposent d'ailleurs l'hypothèse que concentrer les coupes intensives dans de petits espaces réduits leur impact.

L'effet des coupes forestières dépend grandement de l'intensité de prélèvement du traitement, notamment de l'ouverture de la canopée après intervention. Selon son intensité, l'ouverture fait varier la luminosité au sol (Carlson et Groot, 1997; Semlitsch *et al.*, 2009) et induit ainsi un changement de la température (Harpole et Haas, 1999). L'augmentation des températures au sol, dans les traitements forestiers, constitue l'une des principales sources de disparition des salamandres puisqu'elles sont intolérantes aux températures élevées (Herbeck et Larsen, 1998; Knapp *et al.*, 2003). En effet, la chaleur accentue le risque de dessiccation et augmente les demandes métaboliques (Homyack *et al.*, 2011). Harpole et Haas (1999) ont observé que la température au sol était plus élevée pour les traitements de coupes totales, de coupes progressives et de coupes partielles que dans les forêts témoins. De plus, l'augmentation de la température et de la sècheresse a un impact important sur les juvéniles puisqu'ils ont un rapport surface:volume plus élevé que les adultes (Homyack et Haas, 2009). Ceci peut réduire le taux de recrutement de cette classe d'âge dans les populations. À l'inverse, les coupes avec une forte proportion de couvert forestier favorisent l'humidité de la litière, ce qui augmente la probabilité de présence de salamandres (Harpole et Haas, 1999). Finalement, la litière peut être affectée par l'âge de la coupe forestière, ce qui peut à son tour limiter l'abondance des salamandres (Ash, 1995). Harper et Guynn (1999) ont montré que l'épaisseur de la litière dans des coupes de 0 à 12 ans était significativement inférieure à celle retrouvée dans des coupes âgées de 14 à 39 ans. Toutefois, l'épaisseur de la litière peut aussi dépendre de la présence de vers de terres exotiques. Effectivement, ces derniers diminuent l'épaisseur de la litière ce qui peut nuire aux vertébrés qui en sont dépendants, telles que les salamandres terrestres (Maerz *et al*., 2009).

Une des caractéristiques importantes des coupes progressives irrégulières est la préparation du terrain, appelé le scarifiage. Cette technique consiste à mélanger la première couche organique du sol avec 5 cm de couche minéral. La superficie de sol scarifiée dépend du type de CPI. Cette préparation du sol peut avoir un grand impact sur les galeries utilisées par les salamandres ainsi que de la disponibilité des débris ligneux puisque ceux-ci sont déplacés.

Effets des traitements sylvicoles sur la disponibilité des débris ligneux

La plupart des traitements sylvicoles diminuent le volume de vieux débris ligneux âgés retrouvés en forêt, autant pour les chicots que les débris au sol (Gore et Paterson*,* 1985 ; Spies *et al*., 1989) au détriment de plusieurs espèces animales et végétales (Warren and Key, 1991; Bernes, 1994). Les débris ligneux représentent l'une des composantes des écosystèmes les plus importantes et les plus négligées (Harmon *et al.*, 1986). Ils détiennent des rôles importants quant à la dynamique de l'écosystème, par exemple en contrôlant l'érosion et le drainage du sol (Stevens, 1997). Ce changement dans la quantité de débris ligneux nuit aux écosystèmes de diverses façons, notamment en modifiant les relations prédateurs-proies et les dynamiques de populations (Jonsell, 2007; Rifell *et al.,* 2011). La perte de cette matière ligneuse au sol nuit aussi aux petits animaux tels que les micromammifères (Bowman *et al.*, 2000), les amphibiens et les reptiles (Demaynadier et Hunter, 1995; Russell *et al.*, 2004).

L'abondance des salamandres est étroitement liée à la densité de débris ligneux au sol (Demaynadier et Hunter, 1995; McKenny *et al.*, 2006; Semlitsch *et al.*, 2009) et certains ont trouvé une corrélation entre la longueur des débris ligneux et la probabilité d'y trouver des salamandres (Strojny et Hunter, 2009). Les débris ligneux sont utilisés pour la nidification, l'alimentation et comme refuge (Otto *et al.*, 2013). La présence de débris ligneux dans les sites perturbés par la foresterie peut amoindrir les effets négatifs des coupes forestières à court terme (McKenny *et al*., 2006; Otto *et al.*, 2013), particulièrement les débris ligneux âgés, bien dégradés et de grande taille, puisqu'ils représentent un environnement plus stable que les petits débris ligneux (Petranka *et al.*, 1994; Bunnell et Houde, 2010). Gore et Patterson (1985) ont montré que les coupes totales et les coupes partielles peuvent réduire l'accumulation de débris ligneux, mais que les coupes forestières avec une longue période de régénération produisent des densités de débris ligneux similaires à celles retrouvées en vieilles forêts. Les pratiques sylvicoles qui conservent les débris ligneux au sol peuvent également aider à maintenir un environnement viable pour les amphibiens (Moseley *et al.*, 2004).

Quoi qu'il en soit, les salamandres ayant survécu à une perturbation peuvent quitter leur territoire à la recherche d'un habitat moins perturbé, survivre sous les débris ligneux restants ou s'enfouir plus profondément dans le sol (Fraser, 1976; Jaeger, 1980). Par contre, les probabilités d'y trouver des proies intéressantes ou de se reproduire sont plus faibles qu'en surface (Jaeger, 1980). Cela peut induire une diminution du nombre de femelles gestantes et des juvéniles dans une population en plus de diminuer la condition corporelle des individus (Homyack et Haas, 2009). La connaissance de ces caractéristiques de populations est essentielle pour dresser un portrait des populations de salamandres cendrées et ainsi quantifier l'effet des coupes forestières sur cette espèce.

Une tendance en émergence en herpétologie: l'estimation de la détection imparfaite des individus

La détection imparfaite est un élément important à considérer lors d'études de populations d'amphibiens. Comme mentionné plus haut, les salamandres se retrouvent à la surface du sol seulement lorsque les conditions sont optimales, autrement, elles sont souterraines (Petranka, 1998; Bailey *et al.*, 2004). Lors d'études de populations, plusieurs éléments peuvent affecter l'observation de l'espèce visée. Certains éléments affectent le processus biologique en influençant l'abondance ou la présence d'une espèce alors que d'autres agissent sur le processus d'observation en modifiant la probabilité de détecter les individus (Fig. 1). Dans le cas de l'étude des salamandres terrestres dans les coupes forestières, le processus écologique d'intérêt est l'abondance de l'espèce, qui peut varier dépendamment du site ou des coupes forestières (Fig. 1). Le processus d'observation implique une détection imparfaite et peut être influencé par plusieurs variables telles que le moment de la journée, les conditions météorologiques et la méthode d'échantillonnage (Fig. 1).

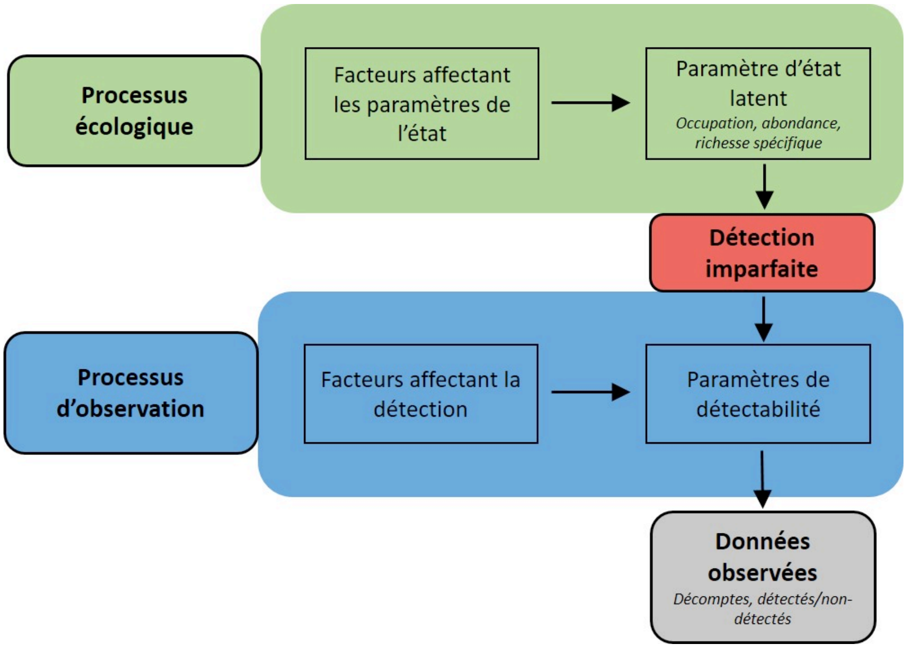

Figure 1. Structure générale des données observées lors d'études terrain. Schéma modifié d'O'Donnell et Semlitsch (2015).

De plus en plus, la détection imparfaite est prise en compte en herpétologie (O'Donnell, 2015). Il est pourtant difficile de comparer les décomptes entre espèces, sites, années, types d'habitats et études en faisant abstraction de la probabilité de détection imparfaite (Mazerolle *et al.*, 2007). Il est essentiel d'estimer la probabilité de détection, surtout dans une étude où l'objectif est d'estimer l'abondance. Plusieurs approches ont été développées en écologie animale afin de pallier ce problème (Mazerolle *et al.*, 2007; Mazerolle, 2015), telles que les méthodes de capture-marquage-recapture ou d'occupation de site. Certaines analyses permettant d'estimer l'abondance ne nécessitent pas le marquage d'individus (Royle, 2004; Buckland *et al.,* 2001). Ces méthodes peuvent être très pratiques et moins coûteuses pour de petits animaux, dont la probabilité de détection est faible, comme les salamandres terrestres. Un modèle dynamique d'abondance (modèle *N*-mélange) peut être utilisé afin d'estimer l'impact des traitements forestiers sur l'abondance des salamandres cendrées, en prenant en compte la détection imparfaite des individus (Royle, 2004; Dail et Madsen, 2010). Cette méthode permet de comparer les populations de salamandres dans l'espace et dans le temps (Royle, 2004). En effectuant plusieurs visites aux mêmes sites, l'estimation de la probabilité de détection s'améliore ainsi que celle des paramètres démographiques. Un moyen d'augmenter la probabilité de détection est d'augmenter l'effort pour une même population, en augmentant le nombre de visites ou la durée de l'échantillonnage pendant une visite (Williams *et al.*, 2002). Ces visites peuvent être réparties dans le temps ou être effectuées simultanément, en utilisant par exemple deux méthodes d'échantillonnage comme c'est le cas dans notre étude. Ainsi, notre étude bonifie la littérature déjà existante sur les salamandres terrestres puisqu'elle prend en compte la détection imparfaite et apporte conséquemment des estimés de populations plus réalistes.

Objectifs

L'intérêt général de cette recherche est de mieux comprendre l'impact des coupes progressives irrégulières sur l'intégrité écologique d'une forêt aménagée à partir de l'étude des changements d'abondance des populations de salamandres terrestres. Ces travaux s'inscrivent également dans un contexte d'amélioration continue de l'aménagement écosystémique en forêts mixtes et feuillues. De plus, cette étude permettra de dresser un portrait des débris ligneux qui sont laissés au sol après les CPI. Les débris ligneux représentent une ressource naturelle de plus en plus convoitée. En effet, la demande en débris ligneux est en augmentation sur le marché de l'énergie verte (Sullivan *et al.*, 2011; Otto *et al.*, 2013). En quantifiant le volume de débris ligneux dans les différents patrons de coupes de CPI, nous pourrons estimer l'impact du volume de débris sur l'état des populations des salamandres terrestres. Ainsi, nous pourrons informer la gestion de cette ressource sur des bases quantitatives plus robustes.

L'objectif global de ce projet de recherche est de déterminer l'impact des CPI sur les populations de salamandres cendrées. Les deux objectifs spécifiques sont:

1. D'évaluer la réponse démographique (survie apparente, recrutement, abondance) de salamandres juvéniles et des salamandres adultes à trois types de CPI.
2. D'évaluer la condition corporelle des salamandres en fonction des trois types de CPI.

Les hypothèses générales sont les suivantes:

- L'abondance des salamandres est plus faible dans les peuplements avec traitements sylvicoles plus intensifs, tels que les CPI par bandes, car ceux-ci diminuent l'épaisseur de la litière et l'humidité au sol et augmentent l'ouverture de la canopée ;
- Une plus faible proportion de la population est constituée de juvéniles dans les traitements sylvicoles les plus intensifs (lisières et trouées), puisque ceux-ci contiennent moins de vieux débris ligneux ;
- Les conditions environnementales plus difficiles (grande ouverture de canopée, faible humidité du sol et épaisseur de litière) dans les traitements sylvicoles les plus intensifs

produisent des individus avec une condition corporelle plus précaire que dans les forêts témoins.

Nous émettons également une hypothèse quant à la détection imparfaite des salamandres terrestres ;

- La probabilité de détecter des individus dans les parcelles est plus élevée lorsque les conditions météorologiques (lors des inventaires et précédant les inventaires) sont propices à l'activité en surface des salamandres, telles qu'un substrat mouillé et des précipitations 48 heures avant l'inventaire (Grover, 1998).

Le deuxième chapitre, *Woodland salamander population dynamics and body condition under irregular shelterwood systems*, est rédigé sous forme d'article scientifique qui sera soumis à la revue *Forest Ecology and Management* avec les auteurs suivant: Mathilde Lapointe St-Pierre, Louis Imbeau et Marc J. Mazerolle.

Chapitre 2. Woodland salamander population dynamics and body condition under irregular shelterwood systems

Résumé

Un des principes de l'aménagement forestier écosystémique consiste à émuler les perturbations naturelles lors des activités de récoltes forestières. Les coupes progressives irrégulières (CPI) sont un nouveau type de traitement sylvicole prometteur en forêt mixte, mais leurs conséquences sur la biodiversité sont méconnues. La salamandre cendrée (*Plethodon cinereus*)*,* étroitement liée aux débris ligneux, joue un rôle important dans l'écosystème des sols forestiers. Le but de ce projet était de déterminer l'impact de trois types de CPI (coupes en lisière, en trouée et en micro-peuplement), relativement à des sites témoins, sur les dynamiques de populations et la condition corporelle de salamandres cendrées. En tout, 64 sites de la région du Témiscamingue ont été échantillonnés à 10 reprises réparties durant l'été 2015 et 2016 dans lesquels deux méthodes d'échantillonnage ont été testées soit les refuges artificiels et des quadrats d'échantillonnage. Les analyses de dynamiques d'abondance ont montré que l'abondance des salamandres des individus ne variaient pas selon les trois différents patrons de coupes de CPI, ni selon les paramètres environnementaux mesurés. Par contre, nos résultats montrent des effets annuels: la condition corporelle des adultes était supérieure en 2015 qu'en 2016 et la probabilité de détection des salamandres adultes était plus élevée en 2016. Pour les juvéniles, leur condition corporelle diminuait avec la progression de la saison et elle était la meilleure dans les traitements en plein et était la plus faible dans les trouées. Ces résultats suggèrent globalement que les CPI maintiennent les attributs d'habitat nécessaires au maintien des populations de salamandres cendrées, 5 à 7 ans après la première coupe.

Abstract

Ecosystem-based management aims to preserve old-growth forest attributes using techniques mimicking natural disturbances. Irregular shelterwood logging is a new method applied to mixed forests, but its impacts on forest floor organisms are poorly known. The aim of this study was to quantify the effects on the population dynamics and body condition of a terrestrial salamander, the red-backed salamander (*Plethodon cinereus*) in three different treatments of irregular shelterwood (strips, uniform and gaps) 5 – 7 years following harvesting compared to old-growth forest controls. A total of 64 sites in the Témiscamingue region were sampled on 10 occasions during the summer of 2015 and 2016. Two sampling methods were tested, namely artificial refuges and sampling quadrats. Analyses showed that salamander abundance and body condition of individuals did not vary according to the three different irregular shelterwood patterns or the environmental parameters measured at the sites. However, the body condition of adult salamanders was lower in 2016 than in 2015 and the detection probability of adult salamanders was greater in 2016 than in 2015. The body condition of juvenile salamanders decreased with increasing Julian day and the body condition of juveniles was also highest in uniform treatments and lowest in gaps treatments. We conclude that environmental conditions 5 to 7 years following treatments in the three patterns of irregular shelterwood harvesting are similar to controls in terms of their capacity to support terrestrial salamander populations.

Introduction

In the context of improving ecosystem-based management, irregular shelterwood systems have recently been proposed for forest stands that are affected by partial stand mortality and subject to gap dynamic processes (Raymond *et al.*, 2009, 2017). Indeed, this silvicultural method can maintain and restore irregular stand structures, by a series of partial cuts (Raymond *et al.,* 2009; Lussier and Meek, 2014), which can produce stands with 2 to 4 age groups (Schütz, 2001; Kelen and Lessard, 2004; Raymond *et al.,* 2009). Hardwood and mixed forests of northeastern North America, where gap dynamics processes are the main natural disturbances, are particularly well suited for the implementation of irregular shelterwood systems (ISS). In these forests, gaps are small and result in uneven-aged stands (Lorimer and Frelich, 1994).In such forests, irregular shelterwood treatments could maintain a large proportion of native biodiversity, increase the long-term sustainability of forest management and be a good alternative to clearcutting for regenerating balsam fir-yellow birch stands (Raymond et *al.*, 2009; 2017). This is especially the case when objectives of the ISS is to maintain a minimal volume of coarse woody debris (CWD) beyond critical thresholds required by several organisms such as amphibians.

The density of CWD is closely related to the abundance of amphibians (DeMaynadier and Hunter, 1995; McKenny *et al.*, 2006; Semlitsch *et al.*, 2009), because terrestrial salamanders use CWD as shelter, foraging, and nesting substrates (Otto *et al.*, 2013). The presence of CWD can reduce the negative short-term effects of logging (Gore and Patterson 1985; McKenny *et al.*, 2006; Otto *et al.*, 2013) and may also help maintain a viable environment for amphibians (Moseley *et al.*, 2004). Thus, studying population parameters in relation to CWD is important in the context of future biomass removal as an alternative source of biofuel and the alarming decline of global amphibian populations (Alford and Richards 1999, Houlahan *et al.*, 2000, Stuart et *al.*, 2004). For instance, in Canada, 42% of amphibians are designated as at-risk by the Committee on the Status of Endangered Wildlife (COSEWIC) and their main threat is habitat loss and degradation (Alford and Richards, 1999; Lesbarrères *et al.*, 2014).

Amphibians and terrestrial salamanders in particular, play a key role in forest ecosystems as they are the main predators of the detritivore food web (Burton and Likens, 1975; Hairston, 1987; Hickerson et *al.*, 2017) and represent prey of choice for several animals (Pough *et al.*, 1987). The eastern red-backed salamander (*Plethodon cinereus*) is the most abundant vertebrate in many North American forests (Burton and Likens, 1975; Petranka *et al.*, 1994). The species has a philopatric behavior and a small home range (Yurewicz and Wilbur, 2004). Because they are deprived of lungs, plethodontid salamanders depend on a moist environment that allows gas exchanges for their cutaneous respiration (Heatwole and Lim, 1961). These salamanders occur on the surface of the forest floor when temperatures and humidity are ideal for cutaneous respiration, otherwise they migrate vertically up to 90 cm deep in the ground for long periods (Grizzell, 1949). These vertical migrations follow the seasonal cycle, with more individuals on the surface during spring and fall than summer (Taub, 1961; Fraser, 1976; Jaeger, 1980). These biological characteristics and physiological restrictions make this salamander a fascinating model to study population dynamics (Feder, 1983; Welsh and Droege, 2001), particularly in a context of new sylvicultural techniques, such as irregular shelterwood systems. Since irregular shelterwood is a new forest management strategy, few studies have focused on the quantification of their impacts on ecosystems or on forest floor fauna (Homyack *et al.,* 2011). Demographic studies are particularly important to quantify the effects of such treatments on salamander population structure to better assess their efficiency in mimicking natural disturbances.

The main goal of our study was to quantify the impact of three patterns of irregular shelterwood treatments (expanded gaps, uniform and strip cuttings) on the population structure of eastern red-backed salamanders. We aimed (1) to evaluate the changes in the population dynamics of juveniles and adult salamanders and (2) to evaluate the body condition of salamanders among sylvicultural treatments. We hypothesized that salamander abundance is lower in the intensive treatment, strip cutting, because this treatment reduce habitat quality such as decreasing litter depth or CWD volume. We also hypothesized that fewer juveniles occur in populations found in slow-regeneration treatment such as, strip cutting, than in controls, because smaller salamanders have a potentially lower survival probability in disturbed forest stands due to their higher proportional evaporative water loss than large salamanders (Spight 1968). We also hypothesized that body condition of adult and juvenile salamanders is lower in the strip cuttings. Finally, we hypothesized that the probability to detect a salamander is highest under weather conditions favourable for surface activity of salamanders, especially when sampling periods occur within 48 hours following precipitations.

Methods

Study area

We conducted the study in the Témiscamingue administrative region of western Québec (Canada), within the sugar maple-yellow birch bioclimatic sub-domain (MRNFP, 2003). The study area is located 70 km east of the town of Temiscaming, near Petit Lac Caugnawana (46°36° N, 78°26° W, Fig. 2A). Three different irregular shelterwood treatments were carried out in the study area in winter 2009–2010 (Joanisse *et al.*, 2013). Specifically, a total of 38 ha was then treated by expanded gap cutting, 88 ha by strip cutting, and 27 ha by uniform irregular shelterwood cutting, whereas a total of 62 ha was used as an untreated control. Expanded gaps consisted in creating four gaps per hectare, each having an average size of 400 m^2 from stem to stem. The uniform and strip irregular shelterwood cutting treatments were modifications of the slow regeneration shelterwood treatment (Joanisse *et al.*, 2014). Strips of irregular shelterwood consisted of sequences of three 10-m wide strips, oriented east to west and harvested in multiple passes. The third treatment, uniform irregular shelterwood, was subjected to specific silvicultural prescriptions determined according to the stand unit characteristics (Lussier and Meek, 2014). Site preparation by scarification was applied in three patterns of irregular shelterwood, where regeneration of yellow birch was deficient and where the machinery could move without injuring residual trees. Site scarification was performed to mix the first 5 cm of the litter with the mineral soil. These irregular shelterwood treatments were the first of a planned series of three cuts. For additional details on the irregular shelterwood treatments applied in the study area, see Suffice *et al.* (2015).

We randomly selected 64 sites in our study area: 18 sites of the strip cutting treatment, 18 sites of the expanded gap treatment, 10 sites of the uniform irregular shelterwood, and 18 control sites (Fig. 2B). Each site was of 80 m² and we maintained a minimal distance of 70 m between each site.

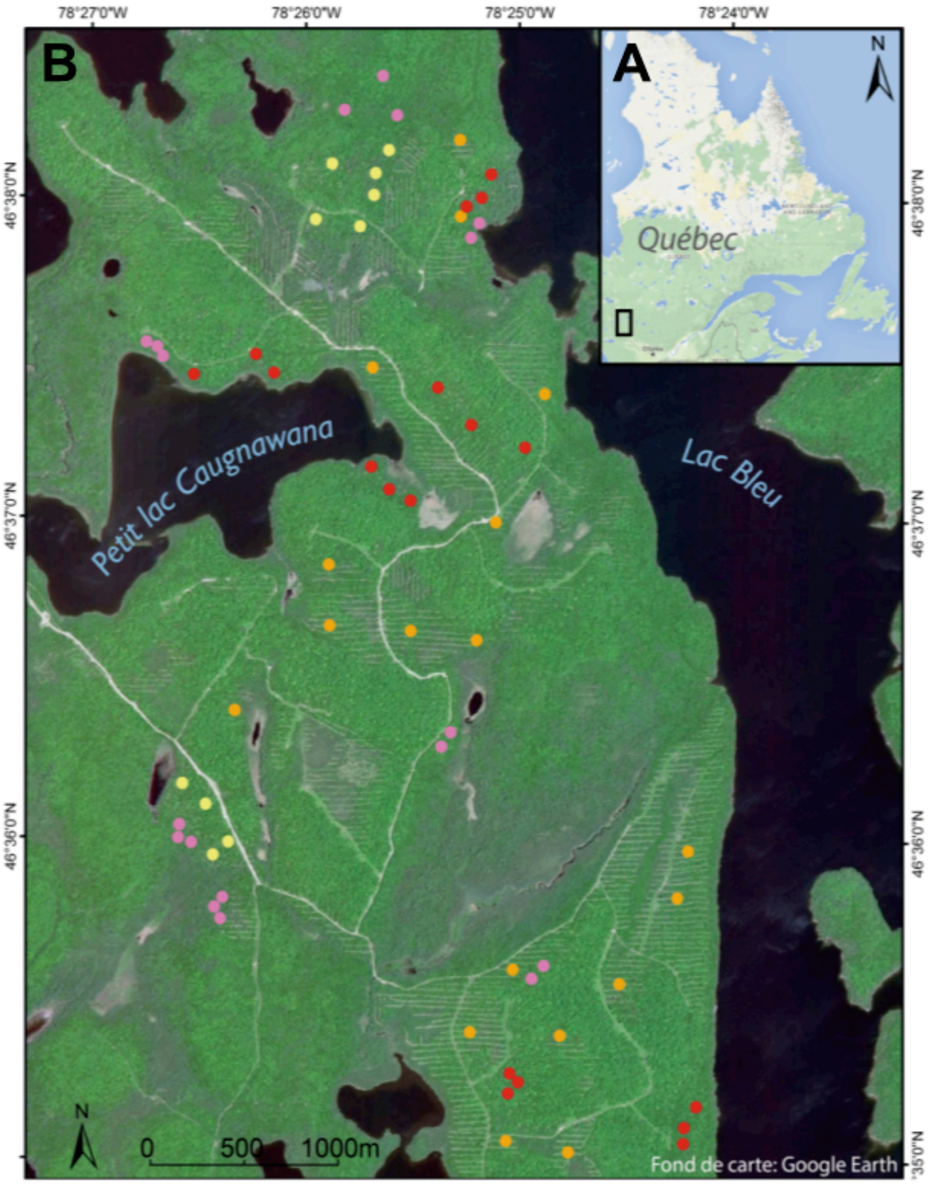

Figure 2. Study area. A) Localization of the Témiscamingue region in western Quebec. B) Distribution of the sites according to irregular shelterwood treatments: expanded gaps (red dots), strip cuttings (orange dots), uniform irregular shelterwoods (yellow dots), and controls (purple dots).

Sampling design

We sampled each site four times in summer 2015 (June 5 – July 28) and six times in the summer of 2016 (May 9 – July 28). The sampling regime was based on Pollock's Robust Design with primary and secondary periods of sampling (Pollock, 1982). Here, primary periods consisted of the four or six visits during 2015 and 2016, respectively. Secondary periods consisted of the two sampling methods used on a given visit (see below). During a given primary period, all sites were visited within 6 days. We separated the 64 sites into 6 areas and visited the sites in a random sequence to avoid visiting the sites in the same order at the same time of day. We maintained 9 days between each primary period in a given year.

On each visit, we employed two sampling techniques at each site to increase salamander detection probability. The first technique consisted of spruce coverboards (25 cm x 30 cm x 2.5 cm) as artificial refugia. Coverboards were deployed in a grid of 3 m x 3 m centered on each site in autumn 2014. We maintained 1 m between adjacent coverboards in a given grid (Fig. 3). The second method consisted of quadrat searches (3 m x 3 m) adjacent to the coverboard grid (Fig. 3). During each visit, we searched the coverboard grid to capture salamanders. We searched a single 3 x 3 m quadrat on each visit, looking under the litter, logs, and rocks (> 5 cm) to find salamanders. We did not tear CWD apart to avoid deteriorating the habitat and cover objects were carefully replaced in their original position after a search. Coverboards were checked within 5 minutes, whereas quadrat searches took between 15 and 20 minutes. Salamanders captured with either sampling technique were temporarily placed in individual plastic bags in the shade to limit desiccation and avoid capturing individuals twice in a sampling session. We weighed salamanders (0.01 g) and measured their snout-vent-length (0.1 mm) (from the snout to the anterior part of the cloaca). Salamanders were classified as adults (> 32 mm) or juveniles (≤ 32 mm; Sayler, 1966). Salamanders were released at their point of capture immediately after the survey.

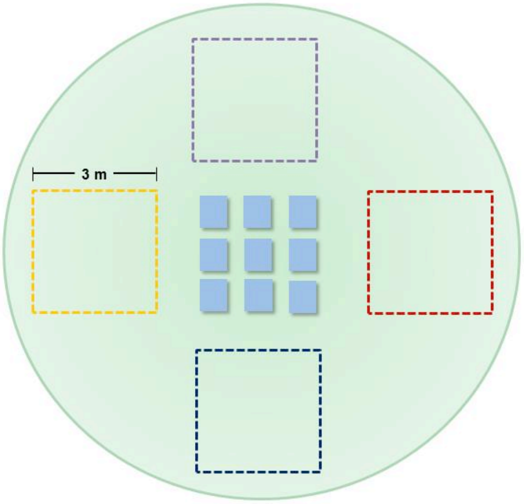

Figure 3. Sampling design representing a coverboard grid in the center of a gap treatment (9 m^2) and the quadrat searches at the periphery of the site (9 m^2). A different quadrat was sampled on each visit in 2015, whereas a quadrat sampled on a given occasion in 2016 could potentially be sampled four primary periods later (drawn to scale).

Site habitat characteristics

We measured basal area (m^2/ha) among treatments in a 400 m^2 plot (11.28 m radius) in which all tree stumps and logs, with a minimum of 10 cm dbh, were classified by tree type (coniferous or hardwood). We visually estimated the vegetation percent cover of grasses, ferns, mosses, shrubs, and bare ground in four subplots (1 m x 1 m) located at each of the four cardinal directions of the site, in the peripheral area of the coverboard grid. We estimated canopy opening at these four points with a spherical densiometer (Model- A). We measured soil compaction using a penetrometer (Model- Geotest E-280 Pocket Penetrometer, USA) at 10 points on the site (two in each subplot and two at the center of the site). The penetrometer gives a resistance measure of the soil surface expressed on a scale from 0 to 5. We measured the litter depth at ten systematic points in each quadrat searched (9 m^2) and coverboard grid.

We measured the basal and apical diameter as well as the length of every CWD found in every quadrat searched. We only measured parts of the CWD that were within the quadrat limits. We assigned all woody debris (stumps and logs > 5 cm) to early- or late-decay classes, adapted from Fauteux *et al.,* (2012). Woody debris in the early-stage decay class had at least a few branches, with or without bark, were hard (> 75%), round, and the tip of a knife could penetrate < 0.5 cm into the wood. The late-stage decay class included soft or very soft and deformed woody debris, often without branches, and a knife could penetrate > 5 cm into the wood. We applied the conic–

paraboloid formula (Equation 1. in Fraver *et al.*, 2007) to estimate the volume of each CWD found in the quadrats searched. Thereafter, we calculated the mean of all the quadrats to obtain a single value per site.

Eq 1. $\text{Volume} = L/12 * (5\ A_b + 5A_u + 2 * \text{sqrt}(A_b * A_u))$

Where;
L represents log length,
$\mathbf{A_b}$ represents the cross-sectional area at the base,
$\mathbf{A_u}$ represents the cross-sectional area at the upper end.

Weather variables

We measured soil humidity systematically in 10 points within the 9 m^2 quadrat searched during each visit with a moisture meter (Model- MMH800, General Tools and Instruments, New York, USA). We also measured soil humidity under each coverboard at each visit. We used precipitation data from the weather station Fildegrand located 25 km from our study area (Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques). For each primary period, we summed the total precipitation for the previous 9 day-interval to relate it to demographic parameters. For each visit, we summed the precipitation of the 24 hours previous to the given visit to quantify the effect of precipitation on salamander detection probability.

Statistical Analyses

All statistical analyses were performed in R 3.2.2 (R Core Team, 2016). To avoid multicollinearity, we did not include correlated variables ($|r| \geq 0.7$) in the same models and all variables were standardized to 0 mean and unit variance before analysis. We used linear mixed-effects models implemented in the nlme package to compare environmental variables (e.g., CWD volume, soil compaction) among the four different treatments. We treated the site as a random effect in the models. Then, we assessed differences among treatments with Tukey's honestly significant difference (HSD) multiple comparisons with the multcomp package (Hothorn *et al.*, 2008).

Dynamic N-mixture abundance modeling

Because salamanders predominantly live underground, those that are captured represent a small portion of the population (Petranka, 1998; Bailey *et al.*, 2004). The number of individuals detected at the surface depends on several factors such as habitat type, time of day, meteorological conditions, sampling method, and observer (O'Donnell and Semlitsch, 2015). Thus, it is difficult to estimate and compare the real salamander abundance between sites, studies, years, and habitat, without accounting for the imperfect detection probability (Mazerolle *et al.*, 2007). Several approaches have been developed in animal ecology to correct this problem and some are specific to amphibians (Mazerolle *et al.*, 2007; Mazerolle, 2015; O'Donnell *et al.*, 2015). Given that we were interested in abundance and changes in abundance between visits, we used dynamic *N*-mixture models to estimate the salamander abundance among treatments. This model type uses counts of unmarked individuals as the raw data and describes population change between seasons while simultaneously accounting for the imperfect probability of detection (Royle, 2004; Dail and Madsen 2010). The model estimates four groups of parameters. Three parameters are related to population size and dynamics, namely, abundance in the first primary period (λ), recruitment rate (γ), and apparent survival (1 – deaths and emigrations) (Ω). The fourth parameter is the probability of detecting an individual during a sampling occasion given it is present (p).

Estimation of salamander population dynamics

Each sampling season in our study followed a robust design allowing the estimation of changes in abundance between visits in a given year. We combined count data from different years in the same model to estimate differences among years and we analyzed juveniles and adults separately. We grouped variables into four biological hypotheses on the salamander population parameters: treatment hypothesis, forest floor quality hypothesis, forest vegetation hypothesis, and weather hypothesis (see Appendix 1). Models testing the treatment hypothesis included the treatment corresponding to the different irregular shelterwood treatments (expanded gap, uniform, strip cutting, and control). Models testing the forest floor quality hypothesis consisted of the CWD volume, the litter depth, and soil compaction. To test the forest vegetation models, we considered the basal area, the percentage of shrub cover, and the percentage of canopy opening. The fourth group of variables consisted of weather conditions during 9 days prior to sampling and focused on total precipitations and average air temperature for this period. For the detection probability parameter, we considered five variables potentially influencing salamander detection probability, based on the literature: the air temperature during the sampling visit, the total precipitation during 24 h prior to sampling, the soil compaction, the CWD volume, and the sampling method (coverboard, quadrat search).

We added a year hypothesis to test differences in estimates of demographic and detection parameters. To avoid overfitting our models, we tested a single hypothesis on a single population parameter at a time while holding the other two parameters constant and tested a hypothesis on detection probability. For adults and juveniles, we tested the hypotheses on the population and detection probability parameters by developing 91 *N*-mixture dynamic models, including a null model (Appendix 2). Parameters were estimated with maximum likelihood in the unmarked package (Fiske and Chandler 2011). We checked model goodness-of-fit using a parametric bootstrap approach based on the Pearson chi-square with 1000 iterations (Mazerolle, 2016). We used a model selection and multimodel inference approach based on the quasi-likelihood Akaike information criterion corrected for small samples ($QAIC_c$) implemented in the AICcmodavg package (Burnham and Anderson 2002, Mazerolle, 2017). We present model-averaged estimates obtained from the shrinkage estimator (Burnham and Anderson 2002, Lukacs *et al*., 2010).

Estimation of salamander body condition

We used the ratio of the length on the mass as a body condition index for *P. cinereus* (Homyack and Haas, 2009). We quantified variations in body condition of the different salamanders captured among different shelterwood treatments using linear mixed models conducted in the nlme package (Pinheiro and Bates, 2000). We analyzed data for adult and juvenile salamanders separately. Because we wanted to test the effect of Julian day on body condition in addition to year, we only analysed data that coincided with the same sampling period in both years (June – July). We considered groups of variables similar to those for the population dynamics analysis (treatment, vegetation, ground, year models) used for the analysis of population dynamics above, but also included the sampling method as an explanatory variable. Because cover objects like coverboards may be a better refugia for salamanders than the litter (Grover, 1998), we expected salamanders under coverboards would have a greater body condition than in the litter (Marsh and Goicochea, 2003). Based on these groups of variables, we formulated 13 candidate models using the site as a random effect (Table 1). Similarly to the previous section, we used a model selection and multimodel inference approach to test our hypotheses.

Table 1. Candidate linear mixed models considered in the analysis of the red-backed salamander (*Plethodon cinereus*) body condition for data collected during 2015 and 2016 in western Quebec, Canada. Note that we included the site as a random effect.

Candidate models	Fixed effects
Null	Intercept only
Global model 1	TREAT + YEAR+ JDAY + METHOD
Global model 2	CWD + BASAL+ COMP + SHRUB + LITTER + METHOD + YEAR + JDAY
Global model 3	CWD+ BASAL + COMP + SHRUB + CANOPY + METHOD + YEAR+ JDAY
Ground and METHOD	CWD + LITTER + COMPACTION + METHOD
Vegetation and METHOD	BASAL + CANOPY + SHRUB + METHOD
TREATMENT +JDAY and YEAR	TREAT + JDAY + YEAR
TREATMENT+ JDAY	TREAT + JDAY
Ground, JDAY and YEAR	CWD + LITTER+ COMPACTION + JDAY + YEAR
Ground and JDAY	CWD + LITTER+ COMPACTION + JDAY
Vegetation + JDAY	BASAL + CANOPY + SHRUB + JDAY
Vegetation, JDAY + YEAR	BASAL + CANOPY + SHRUB + JDAY + YEAR

Results

Environmental characteristics in irregular shelterwood treatments

Environmental characteristics measured 5 to 7 years after treatment varied substantially with irregular shelterwood treatments. Conditions at the control sites, namely, the volume of CWD, the soil compaction, the canopy opening, and the litter depth, differed with conditions in irregular shelterwood treatments (Fig. 4). Control sites had the highest CWD volume (all decay-classes combined) and was different from the three treatments ($F_{3,60} = 8.66$, $P < 0.0001$, Fig. 4A). Soil compaction was lowest in control sites ($F_{3,60} = 18.05$, $P < 0.0001$, Fig. 4B). Canopy opening was the lowest in control sites and the highest in strip cuttings ($F_{3,60} = 84.43$, $P < 0.0001$, Fig. 4C). Shrub cover reached the highest levels in expanded gap treatments and the lowest in uniform treatments, whereas controls and the gap treatment had similar levels of shrub cover ($F_{3,60} =$

10.25, *P* < 0.0001, Fig. 4D). The litter depth was the deepest in the control treatment and the shallowest in the strip cutting treatment ($F_{3,60}$ = 56.56, *P* < 0.0001, Fig. 4E). Finally, the basal area was the highest in control sites and the lowest in gap treatment sites, but the uniform treatment did not differ from the control treatment ($F_{3,60}$ = 7.55,, *P* = 0.0002, Fig. 4F).).

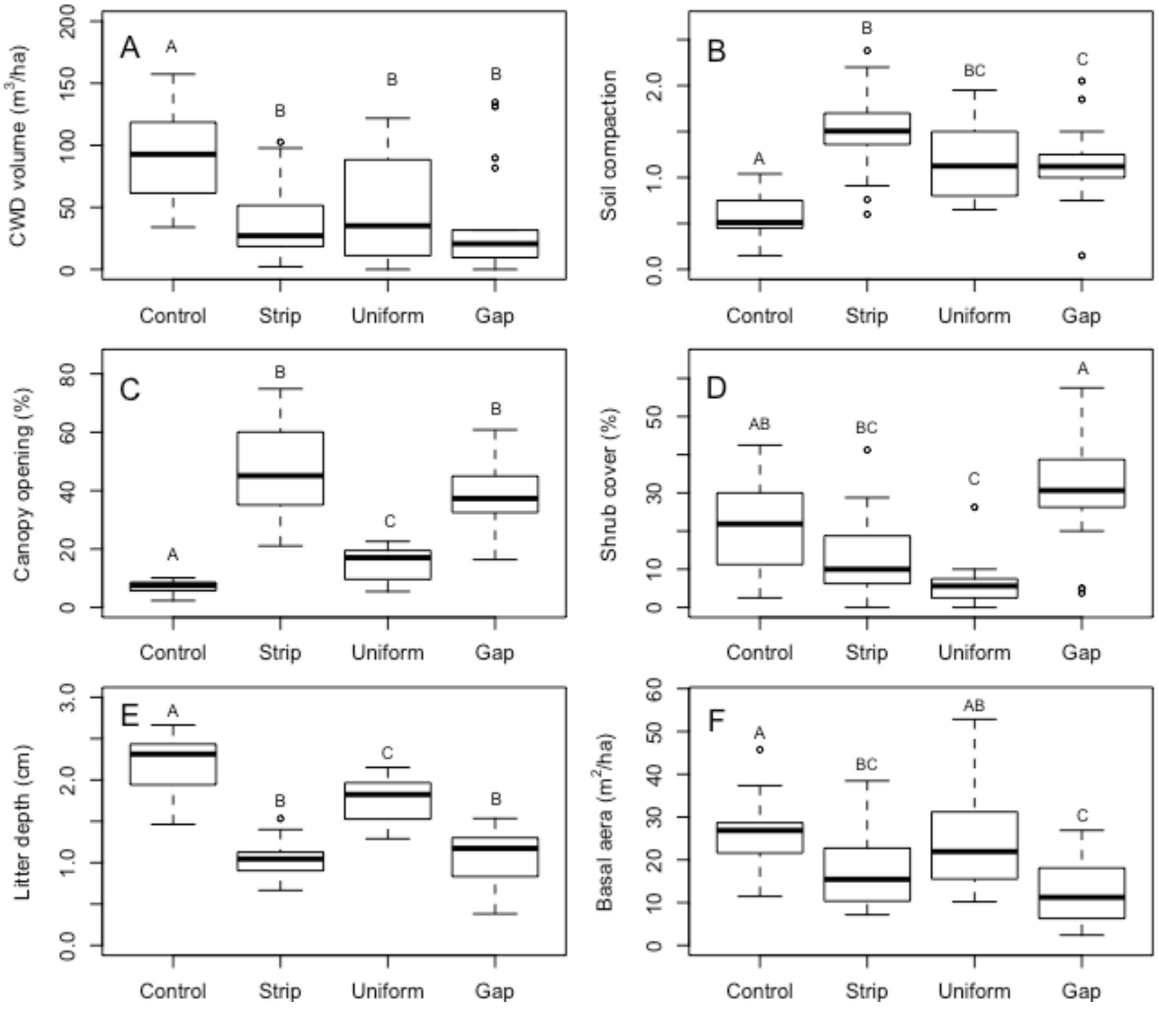

Figure 4. Variability of environmental characteristics potentially affecting salamander population parameters across three different patterns of irregular shelterwood and control sites, in western Quebec, Canada. Letters indicate whether means of treatments estimated from linear mixed models differ (Tukey's HSD test, P < 0.01).

Volumes of early-stage decay CWD did not differ between treatments ($F_{3,\ 60}$ = 0.57, *P* = 0.6364, Fig. 5A). For the late-stage decay class, which is the most important for terrestrial salamanders, the highest CWD volume was in control sites and it differed significantly from the three treatments ($F_{3,\ 60}$ = 17.17, *P* < 0.0001, Fig. 5B).

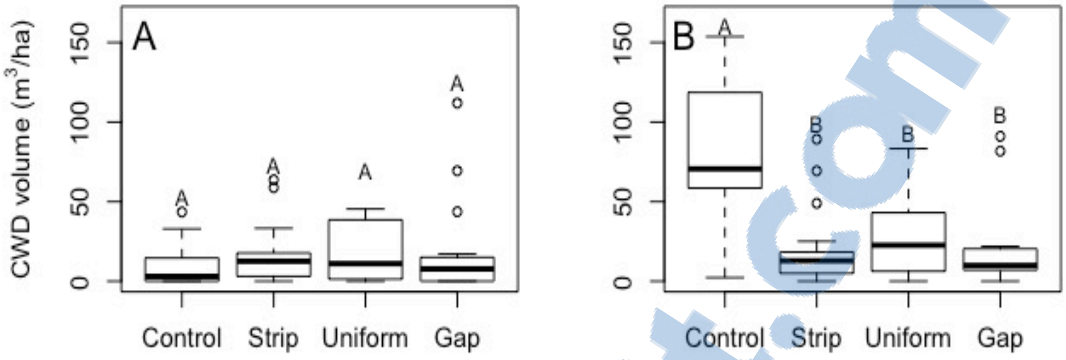

Figure 5. Variability of average CWD volume (m^3/ha) of early-stage decay (A) (B) in three irregular shelterwood treatments and controls in western Québec, Canada. Letters indicate whether means of treatments estimated from linear mixed models differ (Tukey's HSD test, $P < 0.01$).

Salamander captures

We captured a total of 611 salamanders (including recaptures) during the two field seasons. Adults represented 63.2% (386 salamanders) of the individuals captured, whereas juveniles represented 36.8%. Raw captures of juveniles and adults varied with treatment and year (Fig. 6). We captured more adults than juvenile salamanders in every irregular shelterwood treatment. In 2015, we found more individuals in gaps than in control sites (Fig. 6).

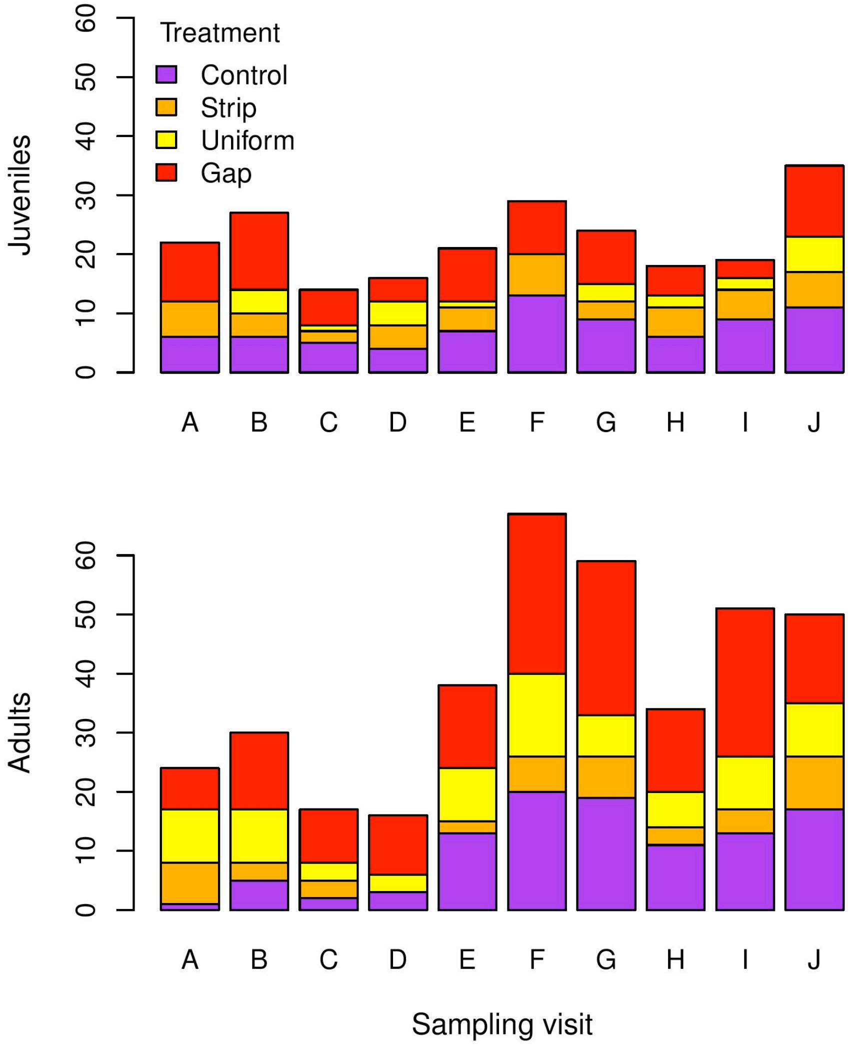

Figure 6. Number of raw captures of juveniles and adults eastern red-backed salamanders (*Plethodon cinereus*) during the four primary visits in 2015 (A, B, C, D) and the six primary visits in 2016 (E, F, G, H, I, J), in irregular shelterwood treatments (strip, uniform irregular shelterwood, gap) and control sites.

Salamander population dynamics

The analysis of the adult segment of the salamander population revealed that two models emerged from the candidate models. The top-ranked model ($\omega = 0.37$) allowed apparent survival to vary with treatment, whereas detection probability included the effects of year and sampling method (Table 2). This model was followed closely by the model that included the same structure on detection probability, but with treatment effects on recruitment ($\omega = 0.35$).

Table 2. Model selection of the *N*-mixture models for the count data of the adult age class based on the QAIC$_c$ collected in 2015 and 2016 in western Quebec, Canada. Delta QAICc (Δ QAIC$_c$) denotes the distance between each model and the top-ranked model, QAIC$_c$ weight (ω) corresponds to the proportion of support in favor of each model, K is the number of estimated parameters in the model. The estimate of c-hat (1.18), obtained from 1000 parametric bootstrap iterations, was used to adjust model selection.

Candidate models	**K**	**QAIC$_c$**	**ΔQAIC$_c$**	**ω**
λ(.) γ(.) Ω(TREAT) p(YEAR+ METHOD)	10	1479.42	0.00	0.37
λ(.) γ(TREAT) Ω(.) p(YEAR+ METHOD)	10	1479.52	0.10	0.35
λ(CWD + LITTER + COMPACTION) γ(.) Ω(.) p(YEAR+ METHOD)	10	1482.16	2.75	0.09
λ(TREAT) γ(.)Ω(.) p(YEAR)	9	1483.13	3.71	0.06
λ(.) γ(TREAT) Ω(.) p(YEAR+ METHOD)	11	1484.12	4.70	0.03
λ(.) γ(.) Ω(TREAT) p(YEAR)	9	1485.03	5.61	0.02
λ(.) γ(TREAT) Ω(.) p(YEAR)	9	1485.16	5.74	0.02
λ(.) γ(.) Ω(CWD + LITTER+ COMPACTION) p(YEAR+ METHOD)	11	1486.68	7.26	0.01

Following multimodel inference, there was no evidence for variation of either recruitment or apparent survival among the 3 treatments relative to the controls, as the unconditional 95% confidence intervals largely overlapped 0 for γ (model-averaged β_{strips}: -0.25, 95% CI: [-1.08, 0.58], model-averaged β_{gaps}: 0.21, 95% CI: [-0.42, 0.85], model-averaged $\beta_{uniforms}$: -0.14, 95% CI: [-0.71, 0.44]) and for Ω (model-averaged β_{strips}: -0.34, 95% CI: [-1.33, 0.66], model-averaged β_{gaps}: 0.42, 95% CI: -0.95, 1.79], model-averaged $\beta_{uniforms}$: -0.24, 95% CI: -1.12, 0.64]). Detection probability was greater in 2016 than 2015 (for p: model-averaged $\beta_{Year2016}$: 0.88, 95% CI: [0.52, 1.24]), but there was no evidence for variation with the sampling method (Fig. 7).

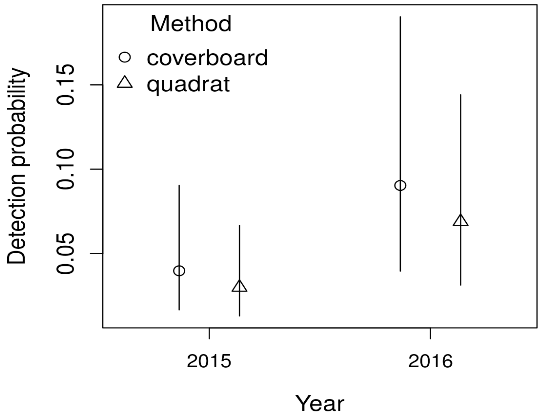

Figure 7. Variation in detection probability of adult eastern red-backed salamanders (*Plethodon cinereus*) with year and search method. Results are based on model-averaged predictions and error bars denote 95% confidence intervals.

Two models emerged among the candidate models for the juvenile count data, both with the same structure on recruitment (Table 3). Specifically, the top-ranked model consisted of ground conditions (CWD volume, forest litter, and soil compaction) on recruitment and included an effect of year on detection probability ($\omega = 0.36$). The second-ranked model included the effect of ground conditions on recruitment, but allowed detection probability to vary with air temperature and total precipitation within 24 h of the sampling visit ($\omega = 0.14$). However, multimodel inference did not suggest any variation of either recruitment or detection probability with the above-mentioned variables, as the 95% unconditional confidence intervals largely overlapped 0 for γ (model-averaged β_{CWD}: -1.78, 95% CI: [-4.73, 1.17], model-averaged β_{litter}: 1.09, 95% CI: [-0.94, 3.13], $\beta_{compaction:}$ -0.92, 95% CI: [-4.22, 2.38]) and for p (model-averaged β_{rain}: 0.03, 95% CI: [-0.09, 0.14], model-averaged β_{air}: 0.01, 95% CI: [-0.09, 0.11], model-averaged β_{year}: 0.13, 95% CI: [-0.29, 0.55]).

Table 3. Model selection of the N-mixture models for the count data of the adult age class based on the QAIC$_c$ collected in 2015 and 2016 in western Quebec, Canada. Delta QAICc (Δ QAIC$_c$) denotes the distance between each model and the top-ranked model, QAIC$_c$ weight (ω) corresponds to the proportion of support in favor of each model, K is the number of estimated parameters in the model. The estimate of c-hat (1.18), obtained from 1000 parametric bootstrap iterations, was used to adjust model selection.

Candidate models	**K**	**QAIC$_c$**	**ΔQAIC$_c$**	**ω**
λ(.) γ(CWD + LITTER + COMPACTION) Ω(.) p(YEAR)	10	1084.06	0.00	0.36
λ(.) γ(CWD + LITTER + COMPACTION) Ω(.) p(RAIN + AIR)	11	1085.96	1.91	0.14
λ(.) γ(CWD + LITTER + COMPACTION) Ω(.) p(YEAR + METHOD)	11	1086.35	2.29	0.11
λ(.) γ(.) Ω(TREE + SHRUB + COVER) p(RAIN + AIR)	10	1087.45	3.40	0.07
λ(TREAT) γ(.) Ω(.) p(YEAR)	9	1087.85	3.78	0.05
λ(.) γ(.) Ω(TREE + SHRUB + COVER) p(YEAR + METHOD)	10	1089.75	3.79	0.05
λ(.) γ(.) Ω(CWD + LITTER + COMPACTION) p(RAIN + AIR + METHOD)	12	1088.30	4.24	0.04
λ(.) γ(CWD + LITTER + COMPACTION) Ω(.) p(CWD + COMPACTION)	12	1088.55	4.50	0.04
λ(.) γ(.) Ω(TREE + SHRUB + COVER) p(RAIN + AIR + METHOD)	11	1089.75	5.69	0.02
λ(TREAT) γ(.) Ω(.) p(YEAR + METHOD)	10	1090.09	6.04	0.02
λ(TREAT) γ(.) Ω(.) p(RAIN + AIR)	10	1090.11	6.05	0.02
Null	5	1090.91	6.85	0.01

Initial abundance and recruitment rate of adult salamander where not different from juvenile initial abundance and recruitment rate, in every treatment (Table 4). Also, we use model-averaged predictions to see that detection of salamanders varied with the sampling method and the year (Table 5).

Table 4. Model-averaged predictions of the population parameters, based on the entire candidate *N*-mixture models and presented for the two age classes of the red-backed salamander (*Plethodon cinereus)* in Western Quebec, Canada in 2015 and 2016.

	Treatments	Initial abundance	CI	Recrutement rate	IC	Apparent survival	CI
Adults	Control	5.29	[2.31, 11.86]	1.20	[0.20, 5.83]	0.728	[0.29, 0.95]
	Uniform	5.22	[2.30, 11.64]	1.007	[0.19, 4.68]	0.674	[0.23, 0.94]
	Strip	5.22	[2.31, 11.59]	0.893	[0.15, 4.61]	0.648	[0.21, 0.94]
	Gap	5.53	[2.24, 12.92]	1.683	[0.21, 9.07]	0.788	[0.26, 0.98]
Juveniles	Control	3.16	[1.48, 6.54]	0.236	[0.01, 5.47]	0.929	[0.45, 1]
	Uniform	2.92	[0.81, 9.16]	0.236	[0.01, 5.47]	0.929	[0.45, 1]
	Strip	3.02	[1.32, 6.58]	0.236	[0.01, 5.47]	0.929	[0.45, 1]
	Gap	3.24	[1.51, 6.72]	0.236	[0.01, 5.47]	0.929	[0.45, 1]

Table 5. Model-averaged predictions of the detection probability, based on the entire candidate *N*-mixture models and presented for the two age classes of the red-backed salamander (*Plethodon cinereus)* and the two sampling methods in Western Quebec, Canada in 2015 and 2016.

	Year	Coverboards	CI	Quadrat	CI
Adults	2015	0.040	[0.02, 0.09]	0.030	[0.013, 0.07]
	2016	0.092	[0.04, 0.19]	0.070	[0.03, 0.15]
Juveniles	2015	0.052	[0.03, 0.105]	0.052	[0.03, 0.105]
	2016	0.060	[0.03, 0.12]	0.059	[0.03, 0.114]

Salamander body condition

Three models had support in explaining the body condition of adult salamanders (Table 6). The model consisting of the treatment, Julian day, and year effects was the most parsimonious with 42% of the weight. However, this model was followed closely by one model consisting of the effects of forest floor characteristics (CWD volume, litter depth, and soil compaction), Julian day, and year ($\omega_i = 0.40$). The third-ranked model consisted of the effects of vegetation, Julian day, and year ($\omega_i = 0.11$) (Table 6). Multimodel inference indicated that the year was the only variable influencing the body condition of adult salamanders, with salamanders in 2016 having a lower body condition than in 2015 (model-averaged $\beta_{Year2016}$: -0.45, 95% CI: [-0.73, -0.17]). . We observed different patterns of body condition for juvenile salamanders. Indeed, the model consisting of the treatment and Julian day effects was the most parsimonious ($w_i = 0.54$) followed by the model consisting of the treatment, the Julian day, and the year ($w_i = 0.24$), and by the global model 1 ($w_i = 0.21$) (Table 6). The body condition of juveniles decreased with increasing Julian day (model-averaged β: -0.22, 95% CI: [-0.39, -0.04]). We also found that the body condition of juvenile salamanders was lower in the strip cutting treatment compared to the control (model-averaged β_{Strip}: -0.35, 95% CI: [-0.68, -0.03]), but that body condition was greater in the uniform treatment than in the control (model-averaged $\beta_{Uniform}$: 0.42, 95% CI: [0.06, 0.79]).

Table 6. Model selection of the linear mixed models of the body condition of adult and juvenile salamanders based on the AIC_c. Delta AIC_c (Δ AIC_c) denotes the distance between each model and the top-ranked model, AIC_c weight (ω) corresponds to the proportion of support in favor of each model, K is the number of estimated parameters in the model.

Age class	Models	K	AIC_c	Δ AIC_c	ω
Adults	TREAT, JDAY + YEAR	9	713.79	0.00	0.42
	GROUND, JDAY + YEAR	8	713.88	0.09	0.40
	VEGETATION, JDAY and YEAR	8	716.38	2.59	0.11
Juveniles	TREAMENT + JDAY	7	321.89	0.00	0.54
	TREATMENT, JDAY YEAR	8	323.53	1.64	0.24
	Global 1	8	323.77	1.88	0.21

Discussion

Population dynamics

We expected eastern red-backed salamander population parameters to be lower in strip cuttings, given the intensity of the local disturbance and the limited movement distance of the species. Indeed, Kleeberger and Werner (1982) found that average daily movement of *Plethodon cinereus* was of 0.43 m during the summer, with a home range of 10-25 m^2, whereas Marsh *et al*. (2004) found that most individuals moved only 2 m from the capture site. In contrast with our first hypothesis, we did not detect a negative impact of irregular shelterwood treatments on adult salamander population parameters (initial abundance, recruitment, and apparent survival) 5-7 years after treatment. Our results are in line with studies that showed that forest harvesting strategies that create uneven-aged structure do not influence salamander abundances on the short-term (Knapp *et al.,* 2003; Morneault *et al.,* 2004; McKenny *et al.,* 2006; Raybuck *et al.*, 2015). Ash (1997) also showed that salamanders returned to pre-disturbance levels 4 to 6 years following clear-cut logging and their reappearance corresponded to the timing needed for the replenishment of the litter layer. Clear-cuts are typically conducted at large scales, but are similar in nature to strip cuttings of a 10 meter width in our study, which still had a lower litter depth than control sites 5-7 years after treatment (Fig.4).

A potential explanation of the absence of an effect of irregular shelterwood is rapid regrowth of the understory vegetation after harvesting (Morneault *et al*., 2004). Indeed, during our two field seasons, we found a high shrub cover (Rubus *sp*.) in our treatments but especially in gap sites (Fig. 4). This rapid growth maintains humidity and low temperatures on the soil surface (Raybuck *et al.,* 2015). Similarly, McKenny *et al.* (2006) found no impact of the uneven-aged treatment harvesting approach they considered (i.e., Structural Complexity Enhancement). They attributed their results to a high well-decayed CWD volume on the soil of their treatment. In our own study, we suggest that the high CWD volume and percent shrub cover retain salamanders in irregular shelterwood sites. Even if late-stage decay CWD volumes and litter depth were highest in the control sites (Fig. 4), models that ranked at first place for adult salamanders did not include CWD and litter variables. If irregular shelterwood treatments have a short-term negative effect on salamander populations, this effect is quite limited in time as our study was completed 5-7 years post-treatment. Moreover, Cantrell *et al.*, (2013) showed no negative short-term responses of species richness, diversity and abundance among two oak regeneration treatments (shelterwood of

30 to 40% of basal area retention and oak-shelterwood) on terrestrial salamanders. Our results concur with their conclusions, suggesting that irregular shelterwood is not detrimental to forest salamanders, and that salamanders have a high resilience to disturbances associated with this harvesting practice.

The models that emerged among the candidate models for adult salamanders differed from those in the analysis of the juvenile data. This suggests that juvenile salamanders do not respond similarly to adults. Indeed, the adult models that ranked highest were the ones with variables associated to forest floor characteristics (CWD volume, forest litter, and soil compaction). Nevertheless, demographic parameters of either adult or juvenile components of the population did not vary with any variables we considered. Home range size of the eastern red-backed salamander varies with sex and age class (Kleeberger and Werner, 1982). Adult salamanders are territorial and defend their refugia from intrusion by other salamanders, including juvenile conspecifics (Gergitz and Jaeger, 1990; Smith and Pough, 1994; Jaeger *et al.*, 1995), which may explain why our top-ranked model for adults included forest floor characteristics. Juveniles who could not defend a territory found themselves by default in litter where they are less conspicuous because of their cryptic color and smaller size (Hyde and Simons, 2001). This point agrees with the study of Marsh and Goicochea (2003) in which they observed more adult eastern red-backed salamanders than juveniles under coverboards. Ovaska and Gregory (1989) also hypothesized that small western red-backed salamanders (*Plethodon vehiculum)* utilize moist microhabitats of leaf litter and that juveniles might be excluded from underground refuges.

Other studies report fewer juveniles in recently harvested sites than in controls, which can indicate a low recruitment rate (Ash *et al.*, 2003; Reichenbach and Sattler 2007; Homyack and Haas, 2009; Hocking *et al.*, 2013). However, our models including explanatory variables on recruitment and apparent survival had no support (Table 3). Interestingly, we found no differences in the estimated demographic parameters between juvenile and adult salamanders across the four treatments. In contrast, Homyack and Haas (2009) studied the impact of 6 oak regeneration treatments on the abundance and reproductive demography of terrestrial salamanders. They observed that forest harvesting had a greater impact on juveniles than on adults, from 1 to 6 years post-treatment. They found that *P. cinereus* had a greater proportion of juveniles in unharvested treatment. If such effects are also present in our mixedwood sites, they must be short-term as we found no evidence of treatment effects on juveniles 5-7 years post-treatment.

Body condition

The models that ranked highly for the body condition consisted of treatments and year variables (Julian day and year). Our results show that body condition of adult salamanders in 2016 was lower than in 2015, which goes against a possible short-term negative treatment effect. This result is in line with Biddle *et al*. (2017) who found a relationship between body growth and seasonal variability of climatic conditions. Biddle *et al*. (2017) observed that salamanders grew more quickly in summer because they have more opportunities for activity on the surface of the forest floor. Different patterns of body condition emerged for juvenile salamanders. Our results show that body condition of juveniles decreased with increasing Julian day (model-averaged β: -0.22, 95% CI: [-0.39, -0.04]), in contrast to Homyack *et al.* (2010), who reported that body condition increased later in the summer. We also found that the body condition of juvenile salamanders was lower in the strip treatment compared to the control (model-averaged β_{Strip}: -0.35, 95% CI: [-0.68, -0.03]), but that body condition was greater in the uniform treatment than in the control (model-averaged β_{Uniform}: 0.42, 95% CI: [0.06, 0.79]). This suggests that juveniles were more vulnerable to certain treatments than adults, but further investigations are required to quantify these relationships with new data.

Quality of forest floor in irregular shelterwood

We did not find evidence that demographic parameters of salamanders vary with the amount of CWD volume within the range we observed at our study sites. Terrestrial salamanders prefer well-decayed woody debris (decay classes 3 to 4) (Aubrey, 1988; DeMaynadier and Hunter, 1995), mostly found in control sites in our study, but those are rare in forest soils that have been harvested, particularly the larger pieces (Bunnell and Houde, 2010). Our study did not find an influence of CWD volume on demographic parameters of salamanders on the forest floor. As proposed by Joanisse *et al*. (2014) the CWD volume found in irregular shelterwood treatments is possibly above a critical amount required to maintain biodiversity of forest floor. Even if irregular shelterwood cutting represents an alternative method that is part of ecosystem based management, and keeps a high CWD volume than other sylvicultural treatments, it includes the use of heavy machinery that can have a negative impact on CWD volume. The heavy machinery can also increase soil compaction (Steinbrenner, 1995), which can limit availability and creation of burrows for mole salamanders (*Ambystoma talpoideum*) (Rothermel and Luhring, 2005). Soil compaction can also restrain vertical migration of plethodontid salamanders, as proposed by Grialou (2000). Even if soil compaction did not have an impact on salamanders in our study, it was higher in strip and gap cutting (Fig. 4).

Detection probability

Our results show that detection probability varies with year for adult salamanders (Table 2, 5, and Fig. 7). This is directly related to our hypothesis that detection varies with season. During the 2016 survey period, we started to collect salamanders one month earlier than in 2015 and we had two primary visits more than in 2015. These early visits in 2016 allowed us to follow the full active period of salamanders, i.e., when they emerge from hibernation and forage for food on the surface. Furthermore, the year effect could be related to annual weather patterns. For instance, the total precipitation in 2015 for June and July was 280.9 mm, whereas it was 324.4 mm in June and July 2016. This highlights the importance of estimating the detection probability to improve estimates of demographic parameters. We found no effect of the precipitation on salamander detection, but other studies report that time since last rain is a good predictor of salamander surface activity (O'Donnell *et al.*, 2014).

In herpetological studies, the low detection probability of amphibians and reptiles make observations of individual difficult and that is why we need to take into account factors that could influence detection probability. In our study, we took into account differences in detection components, such as climatic conditions and sampling methods. Unfortunately, we did not find any evidence of their role in detection. First, we expected a positive effect of precipitation on salamander detection, but our results did not support this prediction. Nevertheless, our results are consistent with existing studies, like Jaeger (1980) who did not find any correlation between the rainfall prior to 24 h and salamander surface density. Secondly, we used two sampling methods to increase the detection probability of salamanders, but our results did not reveal differences in the detection probability among the sampling methods. Advantages of the coverboard method include its ease and speed in checking, its superior probability of detecting salamanders compared to pitfall traps, and minimization of mortality and observer error (Harpole and Haas, 1999; Caruso, 2016). However, coverboards can be a concern in harvested sites, because they can artificially improve the habitat quality of harvesting treatments by increasing cover and their use depends on the availability of natural substrates (Hyde and Simons, 2001; Marsh and Goicochea, 2003). Providing artificial cover 4 to 6 years after treatments at our sites might have accelerated the return of the salamanders, but this should be addressed formally in another study.

Conclusion

The goal of this study was to quantify demographic parameters and body condition of adult and juvenile eastern red-backed salamanders relative to irregular shelterwood treatments and control stands. Our results suggest that adult and juvenile salamanders do not respond similarly to irregular shelterwood treatments, but in both cases we found no differences in terms of abundance, recruitment, apparent survival. We found that the detection probability of adults was higher in 2016 than in 2015, which we attribute to larger amounts of precipitation in the 2016 field season. We also found that the body condition of adult and juvenile salamanders was poorer in 2016 than in 2015. Body condition of juveniles varied among harvesting treatments. Juvenile salamanders had a lower body condition in strip cutting treatments than in controls, and a higher body condition in uniform treatments than controls. Salamanders did not respond to volumes of CWD, potentially because volumes were sufficient in the three irregular shelterwood treatments (gaps, strips and uniforms). Our results suggest that eastern red-backed salamanders are resilient to irregular shelterwood treatments 5 to 7 years post-harvesting.

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Annexes

Appendix 1. Hypotheses tested and associated references with 91 candidate *N*-mixture models to analyse detection data of eastern red-backed salamanders (*Plethodon cinereus*) in western Quebec, Canada, during 2015 and 2016.

Model structure	**Predictions**	**References**
Scenarios applied independently on either one of the parameters of initial abundance (λ), recruitment rate (γ) and apparent survival (Ω)		
(.)	Probability of initial abundance, recruitment rate, and apparent survival are constant.	Null model
Treatment		
(TREAT)	Probabilities of initial abundance, recruitment rate, and apparent survival decrease with the intensity of treatment.	Forestry management impacts microhabitats which can affect salamanders (Ash, 1995; Demaynadier and Hunter, 1995). Salamanders disappear after clearcutting (Petranka, 1993). Partial cuts have also a negative impact on salamander populations (Homyack *et al.,* 2011).
Forest floor		
(CWD + LITTER + COMPACTION)	Probabilities of initial abundance, recruitment rate, and apparent survival increase with downed woody debris and litter depth, and decrease with compaction.	Plethodontid salamanders depend on humid substrates (Heatwole and Lim, 1961), which can be maintained by a litter of good quality (Ash, 1995). Woody debris density is related to salamander abundance (Demaynadier et Hunter, 1995; McKenny *et al.*; 2006; Semlitsch *et al*., 2009). Salamanders use downed woody debris as refugia and a reduction of CWD volume can be deleterious to salamanders (Demaynadier et Hunter, 1995; Russel *et al.*, 2004).
Vegetation		
(TREE + SHRUB + COVER)	Probabilities of initial abundance, recruitment rate, and apparent survival increase with basal area and percent of shrub cover, but decrease with canopy opening.	Terrestrial salamanders are well adapted to old forest components, in particular closed canopy and high basal area (Petranka *et al.* 1994; Pough 1987; Hicks and Pearons, 2002). Depending on canopy opening, the luminosity on the floor will change (Carlson et Groot, 1997; Semlitsch *et al.*, 2009) and promotes the growth of shrub species. Treatments with canopy removal have negative impacts on salamanders (Knapp *et al*., 2003).
Weather conditions		

(RAIN + AIR)	Probabilities of initial abundance, recruitment rate, and apparent survival increase with precipitations, but decrease with air temperature.	Temperature increase is one of the main reasons of the disappearance of salamanders after harvesting because they cannot tolerate high temperatures (Herbeck et Larsen, 1998; Knapp *et al.*, 2003).
Set of scenarios applied on the detection parameter (ρ)		
(.)	Detection probabilities are constant	Null model
(RAIN+AIR)	Detection probabilities increase with rainfall and decrease with air temperature.	Salamanders are found on the soil surface when temperature and humidity are optimal, otherwise, they migrate vertically. (Fraser, 1976; Jaeger, 1980; Petranka, 1998; Bailey *et al.*, 2004). Time since last rain is a good predictor of salamander surface activity (O'Donnell *et al.*, 2014).
(CWD + COMPACTION)	Detection probabilities decrease with downed woody debris and increases with compaction.	There is a correlation between length of woody debris and the probability to find salamanders (Strojny et Hunter, 2009). Terrestrial salamanders prefer well-decayed woody debris because they can hide under and inside them (Corn and Bury; 1991). Soil compaction limits burrow availability to salamanders, when a site is disturbed they can hide in soil if it is not compacted (Rothermel and Luhring, 2005).
(RAIN+AIR+METHOD)	Detection probabilities increase with rainfall and decrease with air temperature. Detection probabilities of red-backed salamanders are not affected by the sampling method.	Salamanders are found in soil surface when temperature and humidity are optimal. If not, they migrate vertically (Fraser, 1976; Jaeger, 1980; Petranka, 1998; Bailey *et al.*, 2004).
(CWD+AIR+METHOD)	Detection probabilities increase with downed woody debris and decrease with air temperature. Detection probabilities of red-backed salamanders are not affected by the sampling method.	
(YEAR)	Detection probabilities vary with year.	Biddle *et al.*, (2017) found that salamanders grow more quickly in summer because they have more opportunities for their activities on

		the forest floor. Also, capture rates differ among years (Raybuck *et al.,* 2015).
(YEAR+METHOD)	Detection probabilities of red-backed salamanders are not affected by the sampling method. Detection probabilities vary with year.	

Appendix 2. List of the 91 candidates N-Mixture dynamics models tested for the eastern red-backed salamanders (*Plethodon cinereus*) in western Quebec, Canada, in 2015 and 2016.

Models	Model group	Initial Abundance (λ)	Recruitment Rate (γ)	Apparent Survival (Ω)	Detection (p)
Null	null	λ (.)	γ (.)	Ω (.)	p (.)
m1a	Treatment	λ (Treat)	γ (.)	Ω (.)	p (Rain + Air)
m2a	Forest Floor	λ (CWD + Litter + Compaction)	γ (.)	Ω (.)	p (Rain + Air)
m3a	Vegetation	λ (Tree + Shrub + Cover)	γ (.)	Ω (.)	p (Rain + Air)
m4a	Precipitation	λ (Rain + Air)	γ (.)	Ω (.)	p (Rain + Air)
m5a	Year	λ (Year)	γ (.)	Ω (.)	p (Rain + Air)
m6a	Treatment	λ (.)	γ (Treat)	Ω (.)	p (Rain + Air)
m7a	Forest Floor	λ (.)	γ (CWD + Litter + Compaction)	Ω (.)	p (Rain + Air)
m8a	Vegetation	λ (.)	γ (Tree + Shrub + Cover)	Ω (.)	p (Rain + Air)
m9a	Precipitation	λ (.)	γ (Rain + Air)	Ω (.)	p (Rain + Air)
m10a	Year	λ (.)	γ (Year)	Ω (.)	p (Rain + Air)
m11a	Treatment	λ (.)	γ (.)	γ (Treat)	p (Rain + Air)
m12a	Forest Floor	λ (.)	γ (.)	Ω (CWD + Litter + Compaction)	p (Rain + Air)
m13a	Vegetation	λ (.)	γ (.)	Ω (Tree + Shrub + Cover)	p (Rain + Air)
m14a	Precipitation	λ (.)	γ (.)	Ω (Rain + Air)	p (Rain + Air)
m15a	Year	λ (.)	γ (.)	Ω (Year)	p (Rain + Air)
m1b	Treatment	γ (Treat)	γ (.)	Ω (.)	p (CWD + Compaction)
m2b	Forest Floor	λ (CWD + Litter + Compaction)	γ (.)	Ω (.)	p (CWD + Compaction)
m3b	Vegetation	λ (Tree + Shrub + Cover)	γ (.)	Ω (.)	p (CWD + Compaction)
m4b	Precipitation	λ (Rain + Air)	γ (.)	Ω (.)	p (CWD + Compaction)
m5b	Year	λ (Year)	γ (.)	Ω (.)	p (CWD + Compaction)

m6b	Treatment	λ (.)	γ (Treat)	Ω (.)	p (CWD + Compaction)
m7b	Forest Floor	λ (.)	γ (CWD + Litter + Compaction)	Ω (.)	p (CWD + Compaction)
m8b	Vegetation	λ (.)	γ (Tree + Shrub + Cover)	Ω (.)	p (CWD + Compaction)
m9b	Precipitation	λ (.)	γ (Rain + Air)	Ω (.)	p (CWD + Compaction)
m10b	Year	λ (.)	γ (Year)	Ω (.)	p (CWD + Compaction)
m11b	Treatment	λ (.)	γ (.)	Ω (Treat)	p (CWD + Compaction)
m12b	Forest Floor	λ (.)	γ (.)	Ω (CWD + Litter + Compaction)	p (CWD + Compaction)
m13b	Vegetation	λ (.)	γ (.)	Ω (Tree + Shrub + Cover)	p (CWD + Compaction)
m14b	Precipitation	λ (.)	γ (.)	Ω (Rain + Air)	p (CWD + Compaction)
m15b	Year	λ (.)	γ (.)	Ω (Year)	p (CWD + Compaction)
m1c	Treatment	γ (Treat)	γ (.)	Ω (.)	p (Rain + Air + Method)
m2c	Forest Floor	λ (CWD + Litter + Compaction)	γ (.)	Ω (.)	p (Rain + Air + Method)
m3c	Vegetation	λ (Tree + Shrub + Cover))	γ (.)	Ω (.)	p (Rain + Air + Method)
m4c	Precipitation	λ (Rain + Air)	γ (.)	Ω (.)	p (Rain + Air + Method)
m5c	Year	λ (Year)	γ (.)	Ω (.)	p (Rain + Air + Method)
m6c	Treatment	λ (.)	γ (Treat)	Ω (.)	p (Rain + Air + Method)
m7c	Forest Floor	λ (.)	γ (CWD + Litter + Compaction)	Ω (.)	p (Rain + Air + Method)
m8c	Vegetation	λ (.)	γ (Tree + Shrub + Cover)	Ω (.)	p (Rain + Air + Method)
m9c	Precipitation	λ (.)	γ (Rain + Air)	Ω (.)	p (Rain + Air + Method)
m10c	Year	λ (.)	γ (Year)	Ω (.)	p (Rain + Air + Method)
m11c	Treatment	λ (.)	γ (.)	Ω (Treat)	p (Rain + Air + Method)
m12c	Forest Floor	λ (.)	γ (.)	Ω (CWD + Litter + Compaction)	p (Rain + Air + Method)
m13c	Vegetation	λ (.)	γ (.)	Ω (Tree + Shrub + Cover)	p (Rain + Air + Method)
m14c	Precipitation	λ (.)	γ (.)	Ω (Rain + Air)	p (Rain + Air + Method)
m15c	Year	λ (.)	γ (.)	Ω (Year)	p (Rain + Air + Method)

m1d	Treatment	λ (Treat)	γ (.)	Ω (.)	p (CWD+ Compaction + Method)
m2d	Forest Floor	λ (CWD + Litter + Compaction)	γ (.)	Ω (.)	p (CWD+ Compaction + Method)
m3d	Vegetation	λ (Tree + Shrub + Cover)	γ (.)	Ω (.)	p (CWD+ Compaction + Method)
m4d	Precipitation	λ (Rain + Air)	γ (.)	Ω (.)	p (CWD+ Compaction + Method)
m5d	Year	λ (Year)	γ (.)	Ω (.)	p (CWD+ Compaction + Method)
m6d	Treatment	λ (.)	γ (Treat)	Ω (.)	p (CWD+ Compaction + Method)
m7d	Forest Floor	λ (.)	γ (CWD + Litter + Compaction)	Ω (.)	p (CWD+ Compaction + Method)
m8d	Vegetation	λ (.)	γ (Tree + Shrub + Cover)	Ω (.)	p (CWD+ Compaction + Method)
m9d	Precipitation	λ (.)	γ (Rain + Air)	Ω (.)	p (CWD+ Compaction + Method)
m10d	Year	λ (.)	γ (Year)	Ω (.)	p (CWD+ Compaction + Method)
m11d	Treatment	λ (.)	γ (.)	Ω (Treat)	p (CWD+ Compaction + Method)
m12d	Forest Floor	λ (.)	γ (.)	Ω (CWD + Litter + Compaction)	p (CWD+ Compaction + Method)
m13d	Vegetation	λ (.)	γ (.)	Ω (Tree + Shrub + Cover)	p (CWD+ Compaction + Method)
m14d	Precipitation	λ (.)	γ (.)	Ω (Rain + Air)	p (CWD+ Compaction + Method)
m15d	Year	λ (.)	γ (.)	Ω (Year)	p (CWD+ Compaction + Method)
m1e	Treatment	λ (Treat)	γ (.)	Ω (.)	p (Year)
m2e	Forest Floor	λ (CWD + Litter + Compaction)	γ (.)	Ω (.)	p (Year)
m3e	Vegetation	λ (Tree + Shrub + Cover)	γ (.)	Ω (.)	p (Year)
m4e	Precipitation	λ (Rain + Air)	γ (.)	Ω (.)	p (Year)
m5e	Year	λ (Year)	γ (.)	Ω (.)	p (Year)

m6e	Treatment	λ (.)	γ (Treat)	Ω (.)	p (Year)
m7e	Forest Floor	λ (.)	γ (CWD + Litter + Compaction)	Ω (.)	p (Year)
m8e	Vegetation	λ (.)	γ (Tree + Shrub + Cover)	Ω (.)	p (Year)
m9e	Precipitation	λ (.)	γ (Rain + Air)	Ω (.)	p (Year)
m10e	Year	λ (.)	γ (Year)	Ω (.)	p (Year)
m11e	Treatment	λ (.)	γ (.)	Ω (Treat)	p (Year)
m12e	Forest Floor	λ (.)	γ (.)	Ω (CWD + Litter + Compaction)	p (Year)
m13e	Vegetation	λ (.)	γ (.)	Ω (Tree + Shrub + Cover)	p (Year)
m14e	Precipitation	λ (.)	γ (.)	Ω (Rain + Air)	p (Year)
m15e	Year	λ (.)	γ (.)	Ω (Year)	p (Year)
m1f	Treatment	λ (Treat)	γ (.)	Ω (.)	p (Year+ Method)
m2f	Forest Floor	λ (CWD + Litter + Compaction)	γ (.)	Ω (.)	p (Year+ Method)
m3f	Vegetation	λ (Tree + Shrub + Cover)	γ (.)	Ω (.)	p (Year+ Method)
m4f	Precipitation	λ (Rain + Air)	γ (.)	Ω (.)	p (Year+ Method)
m5f	Year	λ (Year)	γ (.)	Ω (.)	p (Year+ Method)
m6f	Treatment	λ (.)	γ (Treat)	Ω (.)	p (Year+ Method)
m7f	Forest Floor	λ (.)	γ (CWD + Litter + Compaction)	Ω (.)	p (Year+ Method)
m8f	Vegetation	λ (.)	γ (Tree + Shrub + Cover)	Ω (.)	p (Year+ Method)
m9f	Precipitation	λ (.)	γ (Rain + Air)	Ω (.)	p (Year+ Method)
m10f	Year	λ (.)	γ (Year)	Ω (.)	p (Year+ Method)
m11f	Treatment	λ (.)	γ (.)	Ω (Treat)	p (Year+ Method)
m12f	Forest Floor	λ (.)	γ (.)	Ω (CWD + Litter + Compaction)	p (Year+ Method)
m13f	Vegetation	λ (.)	γ (.)	Ω (Tree + Shrub + Cover)	p (Year+ Method)
m14f	Precipitation	λ (.)	γ (.)	Ω (Rain + Air)	p (Year+ Method)
m15f	Year	λ (.)	γ (.)	Ω (Year)	p (Year+ Method)

Chapitre 3. Conclusion générale

L'objectif de ce projet de maîtrise était de déterminer l'impact à court terme (5 à 7 ans après coupe) des coupes progressives irrégulières sur une espèce de salamandre terrestre abondante sur les sols forestiers, la salamandre cendrée (*Plethodon cinereus*). Les objectifs spécifiques étaient de quantifier la dynamique d'abondance des salamandres adultes et juvéniles (1) et de déterminer si les traitements forestiers avaient un impact sur l'indice de masse corporelle des salamandres adultes et juvéniles (2).

Les principaux résultats de l'étude montrent que :

- Premièrement, il n'y a pas d'effet des coupes progressives irrégulières sur l'abondance, le taux de recrutement, et la survie apparente des salamandres cendrées adultes et juvéniles 5 – 7 après la coupe;
- Deuxièmement, nous avons obtenu une meilleure détection des salamandres adultes en 2016 qu'en 2015;
- Troisièmement, la condition corporelle des salamandres adultes était meilleure en 2015 qu'en 2016. La condition corporelle des salamandres juvéniles était meilleure dans les traitements de coupes progressives irrégulières en micro-peuplement (en plein) et elle était moins bonne dans les traitements par bande. Également, la condition corporelle des juvéniles diminuait avec la progression de la saison

Effectivement, nous n'avons pas trouvé d'effet des coupes progressives irrégulières ni des autres variables d'habitat sur les populations de salamandres. Bien que les conditions environnementales varient entre les traitements de nos sites d'étude, les salamandres des deux groupes d'âge (juvéniles et adultes) ont répondu de la même façon à tous les traitements par rapport aux sites témoins.

Nos résultats montrent que la détection des salamandres terrestres peut varier d'une année à l'autre, d'où l'importance de prendre en compte ce paramètre dans les études de populations d'animaux sauvages. Les précipitations ont été plus abondantes en 2016, ce qui pourrait expliquer l'augmentation de la probabilité de détection des salamandres terrestres par rapport à 2015. Les salamandres cendrées adultes attrapées en 2016 avaient une moins bonne condition corporelle que celles attrapées en 2015. Nos résultats ont révélé des résultats différents pour les salamandres juvéniles. La condition corporelle des salamandres juvéniles diminuait avec l'augmentation du jour julien. De plus, la condition corporelle des salamandres juvéniles dans le traitement par bande était inférieure à celle dans le témoin alors que la condition corporelle des juvéniles dans le traitement en plein était supérieure à celle du témoin (model-averaged β_{Uniform}: 0.42, 95% CI: [0.06, 0.79]). Ceci suggère que les juvéniles sont plus sensibles à certains traitements de coupe progressive irrégulière que les adultes.

Cette étude montre l'importance de distinguer les classes d'âges de l'espèce étudiée dans les études de dynamiques populations. Nous n'avons pas observé les mêmes résultats pour les adultes que pour les juvéniles, bien que nous n'ayons observé aucun effet des variables explicatives sur les paramètres démographiques. Toutefois, les paramètres démographiques des adultes ne différaient pas de ceux des juvéniles.

Puisque notre dispositif expérimental est facilement répétable dans l'espace et dans le temps, nous croyons qu'il serait intéressant de continuer nos recherches à propos de l'impact des CPI sur les amphibiens en incluant d'autres paramètres. Premièrement, il serait intéressant de noter les différences à propos du nombre de femelles gravides au sein d'une population. L'état de gravidité des femelles constitue une information facile à mesurer et l'échantillonnage de salamandres terrestres a souvent lieu au printemps durant la période de reproduction. Cette variable peut être un bon indicateur de la qualité de l'habitat et de la viabilité à long terme des populations (Homyack et Haas, 2009). Pour avoir une étude plus intégrative et qui donnerait un meilleur portait de la santé globale des écosystèmes des sols forestiers, il serait intéressant d'inclure d'autres espèces d'amphibiens ou de reptiles. Les impacts des coupes forestières peuvent varier entre les espèces et les taxons. Pour certains reptiles par exemple, les coupes forestières ont un effet positif puisqu'elles favorisent leur thermorégulation (Rota *et al.*, 2017). Nous avons d'ailleurs noté la présence d'autres espèces lors de nos échantillonnages telles que la salamandre maculée (*Ambystoma maculatum*), la salamandre à points bleus (*Ambystoma laterale),* la grenouille des bois (*Lithobates sylvaticus*), le crapaud d'Amérique (*Anaxyrus americanus*), le triton vert au stade juvénile (*Notophthalmus viridescens*) ainsi que la couleuvre rayée *(Thamnophis sirtalis).* Finalement, il serait intéressant de quantifier les impacts des coupes forestières à plus court terme après perturbations (1 à 5 ans après coupes par exemple). S'il y a des effets observables des CPI, ils pourraient se manifester pendant cette période. Par contre, puisque d'autres coupes sont prévues, il serait important de répéter les mesures dans les années suivant les prochaines coupes.

Recommandations

Nos résultats montrent que les trois patrons de coupes de CPI, n'ont pas d'effet négatif sur les salamandres cendrées, 5 – 7 ans après coupes, et que ces approches s'inscrivent dans l'aménagement écosystémique en se rapprochant des perturbations naturelles retrouvées en peuplements forestiers mixtes et feuillus (Raymond *et al.*, 2015). Pour cette raison, nous recommandons l'utilisation des trois types de coupes sous couvert permanent. Également, ces coupes semblent laisser suffisamment de débris ligneux au sol pour favoriser la survie des salamandres cendrées, ce qui peut être bénéfique pour d'autres taxons, tels que les micromammifères. Par contre, nous ne pouvons pas déterminer si les effets sont les mêmes pour toutes les CPI puisque les intensités de coupes dépendent du peuplement et des objectifs visés. Également notre étude n'évalue pas si les impacts sont les mêmes après les coupes successives qui sont prévues. Il serait intéressant d'évaluer l'impact des CPI selon une intensité de prélèvement plus variée ainsi que de poursuivre le suivi après les 2^e et 3^e coupes prévues aux mêmes sites. Les CPI à régime de régénération lente prélèvent un volume de matière ligneuse plus important que les CPI sous couvert permanent (Raymond *et al*., 2009), c'est pourquoi les conclusions de cette étude ne s'appliquent pas à tout les types de CPI. D'autres recherches seraient à réaliser avant de déterminer si les impacts sont les mêmes lorsque les objectifs de coupes ne sont pas les mêmes, par exemple sous couvert permanent ou non. Également, entre les coupes successives, le recrutement de débris ligneux au sol risque de diminuer, car il y aura moins d'arbres matures dans les sites.

Pour terminer, cette étude est d'un intérêt particulier pour le suivi des populations de salamandres, puisque peu d'études scientifiques quantifient les dynamiques de populations d'amphibiens, actuellement au Québec. Le protocole que nous avons employé s'adapterait facilement à d'autres environnements forestiers pour caractériser la biodiversité des sols forestiers ainsi que la dynamique de population. Ces études pourraient devenir primordiales dans les années à venir considérant la vulnérabilité des populations des salamandres d'Amérique du Nord face à une maladie infectieuse et mortelle, la chytridiomycose des salamandres. Cette maladie causée par un champignon (*Batrachochytrium salamandrivorans*) est retrouvée en Europe, en Australie, en Amérique centrale et elle décime de grandes populations d'amphibiens. Cette maladie, proche du chytride des amphibiens, déjà retrouvée au Canada, s'attaque seulement aux salamandres (Martel *et al*., 2014). Le champignon *B. salamandrivorans* est un pathogène à surveiller puisque s'il est importé en Amérique, il pourrait causer des mortalités de masse dans les populations de salamandres (Martel *et al*., 2014). Ce champignon peut se trouver par exemple sur des salamandres exotiques qui sont importées pour l'herpétoculture.

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