UNIVERSITÉ DU QUÉBEC EN OUTAOUAIS

MÉCANISMES ASSOCIÉS AU SUCCÈS D'ENVAHISSEMENT D'ESPÈCES EXOTIQUES ANIMALES DANS LES HABITATS PERTURBÉS : ÉTUDE DU COMPLEXE DE LIMACES *ARION SUBFUSCUS* S.L. DANS DES HABITATS PERTURBÉS PAR DES COUPES FORESTIÈRES

THÈSE

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Ce doctorat est présenté sous la forme d'une thèse comprenant trois articles et je souhaite préciser mon implication étant donné qu'ils sont cosignés. En tant qu'auteure principale de ces articles, j'ai élaboré les objectifs de recherche et la plupart des protocoles d'échantillonnages, réalisé les analyses statistiques, rédigé les articles et intégré les commentaires de mes coauteurs. L'élaboration des objectifs et la rédaction des articles ont été réalisées en collaboration avec ma directrice de recherche, la Dr Angélique Dupuch, et mon codirecteur de recherche, le Dr François Lorenzetti. La Dr Angélique Dupuch a également participé aux analyses statistiques des trois articles.

Dans le chapitre I, j'ai intégré des données obtenues dans le cadre du projet *essai sur la récolte de la biomasse au Island Lake* par les Drs Lisa Venier et Isabelle Aubin (Centre de Foresterie des Grands Lacs, Ontario), et celles obtenues dans le cadre d'une étude sur l'effet des coupes totales sur la biodiversité animale de la Côte Nord effectuée par la Dr Angélique Dupuch, sous la supervision du Dr Daniel Fortin (Université Laval, Québec), en collaboration avec le Dr Christian Hébert (Centre de foresterie des Laurentides, Québec). Afin d'intégrer ces données, j'ai réalisé de nouvelles analyses et interprétations. Les Drs Isabelle Aubin, Lisa Venier, Daniel Fortin et Christian Hébert ont participé à l'interprétation des données, l'écriture et la relecture de cet article et ils en sont donc coauteurs. Cet article a été soumis dans le journal *Biological Invasions*.

Le Dr Hélène Le Borgne (Institut des Sciences de la Forêt Tempérée, UQO) est coauteure du chapitre II car elle a participé à la récolte des données, à l'interprétation des résultats ainsi qu'à l'écriture et la relecture de cet article.

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RÉSUMÉ

Les invasions biologiques sont considérées comme un facteur majeur de perte de biodiversité et plusieurs dizaines d'hypothèses ont été formulées pour expliquer le succès d'envahissement des espèces exotiques. Parmi celles-ci, l'hypothèse de la perturbation propose que le succès d'envahissement des espèces exotiques soit favorisé par la perturbation de l'habitat. Les mécanismes sous-jacents restent cependant peu documentés, tout particulièrement chez les espèces exotiques animales. Parmi les espèces de limaces exotiques au Canada, le complexe envahissant *Arion subfuscus* (Draparnaud, 1805) sensu lato, s'est rapidement établi dans de nombreux écosystèmes d'Amérique du Nord, tels que les forêts aménagées, mais les mécanismes impliqués dans son succès d'envahissement ne sont pas identifiés. Depuis le 19^{e} siècle, les écosystèmes forestiers sont de plus en plus perturbés par l'exploitation forestière à tel point que les coupes forestières sont devenues plus fréquentes que certaines perturbations naturelles dans plusieurs régions du Canada. L'objectif de ma thèse était de déterminer (1) si les perturbations anthropiques (c.-à-d. coupes forestières) favorisent le succès d'envahissement des espèces animales exotiques (*A. subfuscus* s.l., ci-après *Arion*), (2) par quels mécanismes le complexe d'espèces exotiques envahissantes profite de la perturbation, et enfin (3) si la compétition avec ce complexe peut représenter une menace pour le maintien des espèces indigènes sympatriques (*Philomycus* spp., ci-après *Philomycus*). Dans un premier chapitre, j'ai testé l'hypothèse de la perturbation en déterminant l'effet de l'occurrence d'une perturbation (c.-à-d., coupe forestière), son intensité et le temps depuis son occurrence, sur l'abondance d'*Arion*, un indicateur de son succès d'envahissement. Les résultats provenant de trois écosystèmes forestiers de l'est du Canada révèlent que les coupes forestières, selon leurs caractéristiques (intensité et temps écoulé depuis la coupe), peuvent favoriser le succès d'envahissement d'*Arion*. À la lumière de ces résultats, nous avons proposé un cadre conceptuel de l'hypothèse de la perturbation qui prend explicitement en compte l'effet de l'intensité de la perturbation et du temps écoulé depuis son occurrence sur le succès d'envahissement des espèces exotiques, incluant la manière dont ces deux caractéristiques affectent les conditions biotiques et abiotiques de l'écosystème. Ce cadre, qui peut être appliqué aux espèces exotiques animales et végétales, permet de déterminer plus précisément dans quelles circonstances une perturbation de l'habitat va favoriser les invasions animales. Dans le deuxième et troisième chapitre, j'ai cherché à identifier les mécanismes associés au succès d'envahissement des espèces exotiques animales dans les habitats perturbés. Plus particulièrement, j'ai évalué le rôle des (i) modifications d'attributs de l'habitat générées par la coupe forestière, (ii) des valeurs de traits comportementaux, (iii) de la plasticité comportementale et (iv) de la compétition interspécifique par interférence dans le succès d'envahissement d'*Arion* dans les habitats perturbés par des coupes. Nos résultats suggèrent que les changements d'attributs de l'habitat générés par les coupes favorisent directement ou indirectement le succès d'envahissement des espèces exotiques (*Arion*). Une étude en milieu contrôlé des réponses comportementales d'*Arion* et *Philomycus* à une diminution de l'humidité du sol (phénomène régulièrement observé à la suite d'une coupe forestière) a quant à elle révélé qu'*Arion* n'avait ni un niveau d'audace et d'activité exploratoire (deux comportements qui favorisent le succès d'envahissement), ni une plasticité phénotypique plus élevée que *Philomycus*. Ces résultats suggèrent que des valeurs plus avantageuses ou une plasticité plus importante dans ces comportements chez *Arion* comparativement à *Philomycus* ne sont pas impliquées dans le succès d'envahissement d'*Arion* dans les habitats perturbés par des coupes. Finalement, le comportement de *Philomycus* n'étant pas affecté par la présence d'*Arion*, il est donc peu probable que la compétition interspécifique par interférence puisse avoir favorisé le succès d'envahissement d'*Arion* dans les habitats perturbés, tels que les forêts aménagées, et qu'*Arion* menace le maintien des populations indigènes. Des résultats complémentaires suggèrent toutefois qu'*Arion* pourrait exploiter plus efficacement les ressources que les espèces indigènes puisqu'elle utilisait principalement le refuge le plus proche de la nourriture. Ces résultats suggèrent qu'*Arion* a une plus grande capacité de compétition par exploitation que *Philomycus*. En résumé, la réalisation d'expériences en milieu contrôlé combinée à des prises de données en milieu naturel a permis d'apporter des réponses sur les mécanismes associés au succès d'envahissement des espèces exotiques animales dans les habitats perturbés par des coupes.

Mots clés : invasion biologique, perturbation de l'habitat, traits comportementaux, compétition interspécifique, coupe forestière, limace

ABSTRACT

Biological invasions are considered as a major cause of biodiversity loss and several dozen hypotheses have been formulated to explain alien species invasion success. Among them, the disturbance hypothesis posits that habitat disturbance favours the invasion success of alien species. The underlying mechanisms, however, remain poorly studied, particularly in alien animal species. Among the alien slug species in Canada, the invasive species complex *Arion subfuscus* (Draparnaud, 1805) sensu lato, has become rapidly established in many ecosystems in North America, including managed forests, but the mechanisms involved in its invasion success remain unstudied. Since the 19th century, forest ecosystems have been increasingly disturbed by commercial harvesting. In several regions of Canada, harvesting has now replaced natural disturbances as the primary disturbance. The objective of my thesis was to determine (1) if anthropogenic disturbances (i.e., logging) favour the invasion success of alien animal species (*A. subfuscus* s.l., hereafter *Arion*), (2) how the alien species benefit from the disturbance, and finally (3) if competition with the alien species may threaten the sympatric native species (*Philomycus* spp., hereafter *Philomycus*). In the first chapter, I tested the disturbance hypothesis by evaluating the effect of the occurrence of a disturbance (i.e., logging), its intensity and the time since its occurrence on the abundance of *Arion*, a proxy of invasion success. Results from three forest ecosystems in eastern Canada show that logging can promote *Arion* invasion success depending on its characteristics (intensity and time since logging). In light of our results, we propose a more specific formulation of the disturbance hypothesis, as a conceptual framework, based upon the degree to which biotic and abiotic conditions are altered by a disturbance, according to its intensity and time since its occurrence. This framework, which can be applied to alien animals and plants, provides clear predictions on the conditions under which habitat disturbance promotes the invasion success of alien species. In the second and third chapters, I sought to identify the mechanisms associated with alien animal species invasion success in disturbed habitats. More specifically, I evaluated the role of (i) disturbance-induced habitat changes, (ii) behavioural trait values, (iii) behavioural plasticity, and (iv) interspecific competition by interference in *Arion* successful invasion in logged habitats. Our results suggest that changes in habitat attributes induced by logging may directly or indirectly favour the invasion success of alien species (*Arion*). The study in controlled conditions of the behavioural responses of *Arion* and *Philomycus* to a decrease in soil moisture (which often occurs after forest harvesting) revealed that *Arion* had neither higher boldness and activity-exploratory levels (two behaviours that promote invasion success) nor greater phenotypic plasticity than *Philomycus*. These results suggest that more advantageous values or greater plasticity in these behaviours in *Arion* compared to *Philomycus* are not involved in the invasion success of *Arion* in logged habitats. Finally, the presence of *Arion* did not affect the behaviour of *Philomycus*, suggesting that interspecific competition by interference is unlikely to have favoured *Arion* invasion success in disturbed habitats, such as managed forests, and threatened native species. Additional results, however, suggest that *Arion* may more efficiently exploit the resources than native species since it mainly used the closest refuge for the food source. These results suggest that *Arion* may have a greater ability to compete by exploitation than *Philomycus*. To summarise, the implementation of experiments in controlled conditions combined with data collection in forest ecosystems allowed us to better understand the mechanisms associated with successful animal invasions in logged forests.

Keywords: biological invasion, habitat disturbance, behavioural traits, interspecific competition, forest harvesting, slug

INTRODUCTION

0.1 Les invasions biologiques

L’étude des invasions biologiques débuta au milieu du 20e siècle avec la publication de l’ouvrage *The ecology of invasions by animals and plants* par Charles S. Elton en 1958. C’est toutefois à partir des années 90 que grandit l’engouement scientifique autour des espèces exotiques envahissantes (Gurevitch *et al.*, 2011 ; Richardson et Pyšek, 2008), alimenté par quelques invasions médiatisées comme celle de la perche du Nil (*Lates niloticus*) dans le lac Victoria, ou celle de la moule zébrée (*Dreissena polymorpha*) dans les Grands Lacs d’Amérique du Nord.

0.1.1 Définition et processus

Le processus d’envahissement peut être divisé en une série d’étapes lors desquelles des barrières doivent être franchies (Blackburn *et al.*, 2011). La première étape de ce processus est celle du transport assisté par lequel des individus d’une espèce sont déplacés par l’Homme, de manière délibérée ou accidentelle, hors de leur aire d’origine. Si ces individus ont ensuite l’opportunité de se retrouver dans un nouvel environnement, cette phase sera dite d’introduction. Une fois cette deuxième étape franchie, l’espèce introduite sera qualifiée d’espèce « exotique ». La troisième étape est celle de l’établissement. L’espèce nouvellement introduite devra survivre, s’établir et former une population viable dans la région d’introduction. Finalement, des individus pourront se disperser en dehors de la région d’introduction et former de nouvelles populations viables distantes de celle-ci. C’est la phase d’expansion. Une espèce ayant franchi ces quatre étapes est définie comme espèce « exotique envahissante ».

0.1.2 Conséquences des invasions biologiques

Les impacts des espèces exotiques (envahissantes ou non) peuvent être de différentes natures. Certaines espèces peuvent ainsi entrainer des dommages sanitaires en étant la cause ou le vecteur de maladies chez l’Homme, ou bien encore être à l’origine de blessures (Hulme, 2014). Par exemple, la sève de la Berce du Caucase (*Heracleum mantegazzianum*), espèce herbacée introduite au Québec pour des raisons horticoles, contient des toxines activées par la lumière qui provoquent de graves lésions cutanées. Les pertes économiques et les dépenses financières encourues afin de prévenir, contrôler ou éradiquer ces espèces sont encore peu documentées (mais voir Bradshaw *et al.*, 2016 ; Diagne *et al.*, 2020) mais Colautti *et al.* (2006a) ont estimé les coûts annuels engendrés par 16 espèces exotiques envahissantes au Canada à 17 G$. Parmi ces 16 espèces, la moule zébrée se fixe sur les prises d’eau d’installations publiques ou de centrales électriques, nécessitant d’importantes dépenses afin de nettoyer et déboucher les structures touchées (Connelly *et al.*, 2007 ; Ludyanskiy *et al.*, 1993 ; Pimentel *et al.*, 2005). Les espèces exotiques peuvent finalement entrainer des dommages écologiques car elles peuvent modifier le fonctionnement des écosystèmes (Kenis *et al.*, 2009 ; Sousa *et al.*, 2011) en affectant le régime de perturbation (Brooks *et al.*, 2004), ou bien encore l’organisation et la composition des communautés indigènes par modification de l’abondance de certaines espèces (Hejda *et al.*, 2009 ; Kenis *et al.*, 2009 ; Pyšek *et al.*, 2012 ; Vilà *et al.*, 2011). Elles sont ainsi considérées comme une cause majeure de perte de biodiversité (Murphy et Romanuk, 2014) et seraient impliquées dans 58 % des extinctions chez les plantes, amphibiens, reptiles, oiseaux et mammifères (Bellard *et al.*, 2016). Il est estimé que 16 % des espèces exotiques causeront des dommages sanitaires, économiques et environnementaux (Jeschke et Pyšek, 2018). Au Canada, plus de 1 400 espèces exotiques sont présentes dans les écosystèmes agricoles, forestiers et aquatiques (MacIsaac *et al.*, 2002). Il est donc nécessaire d'identifier les facteurs favorisant leur succès d'envahissement afin de mieux comprendre et prédire les invasions biologiques.

0.1.3 Mécanismes impliqués dans les invasions biologiques

Près de 40 hypothèses ont été formulées par la communauté scientifique pour expliquer le succès d'envahissement des espèces exotiques (Catford *et al.*, 2009 ; Dai *et al.*, 2020 ; Enders *et al.*, 2020 ; Jeschke et Heger, 2018). Toutes ces hypothèses peuvent être représentées sous la forme d'un réseau et regroupées en cinq catégories selon le principal mécanisme mis en avant pour expliquer les invasions biologiques (Enders et *al.*, 2018, 2020). Ainsi, les hypothèses du groupe *propagule* suggèrent que la probabilité qu'une espèce devienne envahissante dépendra du nombre d'espèces ou d'individus exotiques qui sont introduits tandis que celles appartenant au groupe *interaction biotique* et *trait* mettent respectivement en avant le rôle des interactions interspécifiques et des caractéristiques des espèces pour expliquer le succès d'envahissement des espèces exotiques. De nombreuses hypothèses dans le groupe *Darwin* reposent sur une perspective éco-évolutives des invasions biologiques et mettent en évidence l'importance de l'héritage évolutif des espèces et la manière dont ce dernier va façonner les interactions biotiques résultant de l'introduction d'espèces. Plusieurs hypothèses de ce groupe suggèrent ainsi que les espèces exotiques pourront s'établir et potentiellement devenir envahissante si elles occupent des niches différentes de celles des espèces indigènes. Finalement, le dernier groupe d'hypothèses *disponibilité des ressources* associe le succès d'envahissement d'une espèce exotique à son accès aux ressources qui dépend des conditions biotiques et abiotiques. Dans ce groupe, on retrouve l'hypothèse de la perturbation qui propose que le succès d'envahissement des espèces exotiques est favorisé par la perturbation de l'habitat (Elton, 1958 ; Hobbs et Huenneke, 1992). Cette hypothèse est d'actualité puisque les habitats sont de plus en plus perturbés et fragmentés par les activités anthropiques. De plus, l'introduction d'espèces exotiques s'étant accentuée au cours des 19^{e} et 20^{e} siècles à la suite de l'intensification du commerce international et ne présentant pas de ralentissement (Seebens *et al.*, 2017, 2020), il est primordial de déterminer l'effet de ces perturbations sur le succès d'envahissement des espèces exotiques.

0.2 Hypothèse de la perturbation

Plusieurs définitions du terme *perturbation* existent (Grime, 1977 ; Petraitis *et al.*, 1989), mais celle de White et Pickett (1985) est généralement utilisée car elle s'applique aux espèces végétales et animales. Une perturbation se caractérise alors comme n'importe quel évènement relativement limité dans le temps qui modifie l'écosystème, les communautés ou la structure des populations, ainsi que les ressources, la disponibilité des substrats ou l'environnement physique. L'hypothèse de la perturbation repose sur l'idée qu'une perturbation (d'origine naturelle ou anthropique) peut modifier les attributs de l'habitat d'une manière qui n'a pas d'équivalent avec l'histoire naturelle des espèces indigènes. De ce fait, une perturbation qui se distingue du régime de perturbation historique, auquel les espèces indigènes sont adaptées, pourrait altérer la composition des communautés, diminuer la richesse spécifique indigène et créer des opportunités pour les espèces exotiques (Hobbs et Huenneke, 1992). L'hypothèse de la perturbation, initialement développée pour les espèces végétales, a longtemps été soutenue par la communauté scientifique malgré des preuves équivoques et le fait qu'elle n'ait pas toujours été évaluée de manière adéquate (critique formulée par Moles *et al.*, 2012 ; Nordheimer et Jeschke, 2018). La méta-analyse de Nordheimer et Jeschke (2018) révèle qu'elle a majoritairement été testée chez les espèces végétales (75 % des études) et qu'elle est modérément supportée (60 % des études en sa faveur). Notre compréhension du rôle de la perturbation dans le succès d'envahissement des espèces exotiques animales reste donc limitée. Par ailleurs, pour tester cette hypothèse, les études évaluent soit l'effet de l'occurrence d'une perturbation (Jauni *et al.*, 2015 ; Lake et Leishman, 2004 ; Malumbres-Olarte *et al.*, 2014), soit celui de ses caractéristiques (p. ex. intensité, taille, fréquence ; Altman et Whitlatch, 2007 ; Grez *et al.*, 2013 ; Rickart *et al.*, 2011 ; Todd *et al.*, 2008) sur le succès d'envahissement. Ce manque de constance méthodologique pourrait expliquer la variation des résultats d'une étude à l'autre et permet difficilement de déterminer dans quelles circonstances la perturbation va favoriser le succès d'envahissement des espèces exotiques animales.

0.2.1 Mécanismes permettant aux espèces exotiques de profiter de la perturbation

Par sa formulation et les idées sous-jacentes sur lesquelles elle repose (appartenance au groupe *disponibilité des ressources*, Enders *et al.*, 2020), l'hypothèse de la perturbation suggère que le succès d'envahissement des espèces exotiques dans les habitats perturbés est principalement la conséquence du déclin des espèces indigènes. Ce déclin libérerait des ressources (hypothèse *increase resource availability* : Sher et Hyatt, 1999) et créerait des opportunités de niches pour les espèces exotiques (hypothèse *empty niche* : MacArthur, 1970). Ce premier mécanisme est similaire à celui que propose Didham *et al.* (2005) selon lequel les espèces exotiques pourraient profiter indirectement de la perturbation en remplissant les niches laissées vacantes par le déclin des espèces indigènes. L'objectif de Didham *et al.* (2005) était d'expliquer l'apparition conjointe des espèces exotiques envahissantes et du déclin des espèces indigènes dans les habitats perturbés. De ce fait, il ne mentionne pas, tout comme l'hypothèse de la perturbation, un second mécanisme potentiel par lequel la perturbation pourrait directement favoriser le succès d'envahissement des espèces exotiques sans pour autant promouvoir le déclin des espèces indigènes. En effet, la perturbation pourrait modifier les conditions environnementales de manière à les rendre plus favorables pour l'espèce exotique, favorisant ainsi son succès d'envahissement. Ces deux mécanismes par lesquelles la perturbation d'habitat peut favoriser directement ou indirectement le succès d'envahissement des espèces exotiques sont non-exclusifs. En effet, la perturbation pourrait affecter les conditions environnementales de manière à les rendre à la fois plus favorables pour les espèces exotiques et moins favorables pour les espèces indigènes (p. ex. Parker *et al.*, 1993). Comprendre de quelle manière la perturbation favorise le succès d'envahissement des espèces exotiques nécessite donc d'étudier l'effet de cette perturbation sur les conditions environnementales et de connaître les besoins des espèces en matière d'habitat ainsi que leurs caractéristiques (Korsu *et al.*, 2007, 2012).

En particulier, une espèce exotique envahissante pourrait bénéficier de la perturbation par le biais de la plasticité phénotypique, un mécanisme régulièrement mis en avant pour expliquer le succès d'envahissement des espèces végétales (Baker, 1965 ; Richards *et al.*, 2006 ; Wright *et al.*, 2010). La plasticité phénotypique se définit comme la capacité d'un organisme à exprimer différents phénotypes (p. ex. traits physiologiques) en fonction des conditions environnementales (Schlichting, 1986). Comme le propose l'hypothèse de la plasticité phénotypique (Baker, 1965 ; Richards *et al.*, 2006), les espèces exotiques envahissantes posséderaient une plus grande plasticité phénotypique comparativement aux espèces non-envahissantes (c.-à-d. indigènes ou exotiques) ce qui favoriserait leur établissement et leur expansion dans de nouveaux habitats (Ghalambor *et al.*, 2007 ; Matesanz *et al.*, 2010 ; Schlichting, 1986 ; Yeh et Price, 2004) tels qu'après une perturbation. Selon Richards *et al.* (2006), il existe trois scénarii illustrant comment une espèce exotique envahissante peut bénéficier de sa plasticité phénotypique plus importante. Elle peut soit (1) maintenir son aptitude phénotypique quand les conditions environnementales deviennent défavorables contrairement aux espèces non-envahissantes (scénario robuste), soit (2) augmenter de manière plus importante son aptitude phénotypique quand l'environnement devient favorable comparée aux espèces non-envahissantes (scénario opportuniste), soit (3) combiner ces deux capacités et présenter alors une aptitude phénotypique supérieure à celle des espèces non-envahissantes dans tous les environnements (scénario robuste et opportuniste). L'hypothèse de la plasticité a principalement été évaluée chez les espèces végétales (Davidson *et al.*, 2011 ; Funk, 2008 ; Godoy *et al.*, 2011 ; Matzek, 2012 ; Palacio-López et Gianoli, 2011) et est relativement bien supportée par les études empiriques (Torchyk et Jeschke, 2018). Les études comparant la plasticité des espèces exotiques envahissantes à celle des espèces indigènes sont toutefois peu communes chez les espèces animales et portent en grande majorité sur la plasticité dans les traits d'histoire de vie (p. ex. Knop and Reusser, 2012), la morphologie (p. ex. Pujol-Buxó *et al.*, 2013) ou la physiologie (p. ex. Phillips *et al.*, 2020) (Torchyk et Jeschke, 2018). Le rôle de la plasticité comportementale dans le succès d'envahissement des espèces exotiques animales n'a que très rarement été étudié (e.g., Pujol-Buxó *et al.*, 2013 ; Ryan et Gunderson, 2020) même si plusieurs traits comportementaux semblent impliqués dans leur succès d'envahissement (Chapple *et al.*, 2012 ; Holway et Suarez, 1999). L'hypothèse de la plasticité est étroitement reliée à l'hypothèse de l'envahisseur idéal dans laquelle Baker identifiait « *la capacité à produire un grand nombre de graines dans une grande variété de conditions environnementales, être tolérant et plastique* » comme une caractéristique favorisant l'envahissement (Baker, 1965).

Herbert G. Baker a initié la réflexion concernant les traits des espèces pouvant favoriser leur succès d'envahissement en établissant une liste de 12 caractéristiques fréquemment observées chez les espèces envahissantes végétales (p. ex. croissance rapide par le biais de reproduction végétative, grande production et longévité des graines). Selon lui, plus une espèce présente ces caractéristiques, plus elle est susceptible de devenir envahissante. Ses travaux ont ainsi mené à la formulation de l'hypothèse de l'envahisseur idéal selon laquelle le succès d'envahissement des espèces exotiques s'explique par leurs traits dits « idéaux », qui favorisent leur établissement et expansion dans de nouveaux habitats. Des valeurs plus avantageuses dans ces traits chez des espèces exotiques animales comparativement aux espèces indigènes pourraient donc expliquer leur succès d'envahissement dans un nouvel environnement, tel qu'après perturbation. Les différences de traits (p. ex. traits d'histoires de vie) entre espèces exotiques et espèces indigènes ont souvent été proposées comme explication au succès d’envahissement des espèces exotiques végétales (Funk, 2008 ; Kolar et Lodge, 2001 ; Nunez-Mir *et al.*, 2019 ; Rejmanek et Richardson, 1996 ; van Kleunen *et al.*, 2010, 2015) et les études comparant les traits des espèces indigènes à ceux des espèces exotiques envahissantes sont devenues de plus en plus courantes durant les trente dernières années (Pyšek et Richardson, 2007). Aucun consensus ne semble toutefois apparaître, car certaines études ont démontré que les espèces exotiques envahissantes végétales possédaient des valeurs de traits plus avantageuses que celles des espèces indigènes (Godoy *et al.*, 2011 ; Mathakutha *et al.*, 2019 ; Sandel et Low, 2019 ; van Kleunen *et al.*, 2010), et d’autres des valeurs de traits similaires (Sandel et Low, 2019). Chez les espèces animales, plusieurs études ont montré que les espèces exotiques envahissantes étaient plus exploratrices (Bubb *et al.*, 2006 ; Chapple *et al.*, 2011 ; Damas-Moreira *et al.*, 2019 ; Rehage et Sih, 2004), audacieuses (Damas-Moreira *et al.*, 2019 ; Monceau *et al.*, 2015) et agressives (Rowles et O’Dowd, 2007 ; Usio *et al.*, 2001) que les espèces indigènes. Ces comportements peuvent promouvoir l’exploitation des ressources (Pintor et Sih, 2009), ainsi que l’établissement et la dispersion dans de nouveaux habitats (Monceau *et al.*, 2015 ; Rehage et Sih, 2004).

0.2.2 Rôle des espèces exotiques dans le déclin des espèces indigènes dans les habitats perturbés

Le succès d’envahissement et le déclin des espèces indigènes apparaissent souvent conjointement dans les habitats perturbés, si bien qu’il devient difficile d’identifier les mécanismes impliqués dans ce déclin (Didham *et al.*, 2005 ; Gurevitch et Padilla, 2004). Celui-ci pourrait être le résultat de changements des conditions environnementales (idée sous-jacente de l’hypothèse de la perturbation), mais ce n’est pas la seule explication possible. En effet, le déclin des espèces indigènes pourrait également être le résultat d’interactions interspécifiques par prédation ou compétition (Didham *et al.*, 2005, 2007). La compétition peut s’exercer par exploitation, quand une espèce utilise une ressource commune au point de réduire sa disponibilité pour les autres espèces, ou par interférence, quand une espèce empêche une ou plusieurs autres espèces d'accéder ou d'utiliser certaines ressources par des interactions directes (p.ex. par le biais d'agressions) ou indirectes (p.ex. par le biais de mucus). La supériorité compétitive des espèces exotiques comparativement aux espèces indigènes pourrait ainsi contribuer au succès d'envahissement des espèces exotiques dans les habitats perturbés en causant le déclin des espèces indigènes. En effet, la perturbation, en favorisant le succès d'envahissement des espèces exotiques, pourrait augmenter l'ampleur de leurs impacts sur les espèces indigènes dans les habitats perturbés (Didham *et al.*, 2007) et ainsi promouvoir l'exclusion compétitive des espèces indigènes par les espèces exotiques. L'exclusion compétitive d'espèces indigènes par des espèces exotiques envahissantes a été démontrée à de nombreuses reprises (Bøhn *et al.*, 2008 ; Byers, 2000 ; Petren et Case, 1996), mais peu d'études empiriques ont jusqu'à présent déterminé comment les espèces exotiques envahissantes animales interagissent avec la perturbation de l'habitat et le rôle de ces dernières dans le déclin d'espèces indigènes (voir : MacDougall et Turkington, 2005 pour les plantes).

L'hypothèse de la perturbation et le cadre conceptuel développé par Didham *et al.* (2005, 2007) sont nécessaires dans la compréhension actuelle du succès d'envahissement des espèces exotiques et du déclin des espèces indigènes dans les habitats perturbés. Ils restent toutefois largement théoriques et n'identifient pas spécifiquement les mécanismes par le biais desquelles les espèces exotiques pourraient bénéficier des perturbations aux dépens des espèces indigènes. Dans le but de mieux comprendre les invasions animales et afin de prévenir les menaces pour les espèces indigènes, il est primordial d'identifier les mécanismes sous-jacents impliqués dans les réponses des espèces exotiques et indigènes à la perturbation d'une part, et de comprendre le rôle des espèces exotiques dans le déclin des espèces indigènes dans les habitats perturbés d'autre part.

0.3 Modèle biologique et objectifs de la thèse

Cette thèse porte sur les espèces de limaces présentes dans les forêts de l'est du Canada. Près de 40 espèces de limaces sont actuellement recensées au Canada dont près de la moitié sont exotiques (Grimm *et al.*, 2009). Environ la moitié des espèces exotiques causent des dommages en milieu agricole tandis que l'on retrouve près de 1.5 fois plus d'espèces exotiques (18) que d'espèces indigènes (12) dans les milieux forestiers (Grimm *et al.*, 2009). Le complexe envahissant *Arion subfuscus* (Draparnaud, 1805) sensu lato est originaire d'Europe (L'Heureux et Angers, 2018) et a démontré une importante capacité à coloniser et proliférer dans les milieux forestiers du Nord-Est des États-Unis et de l'Est canadien. Ce complexe a été recensé pour la première fois au milieu du 19e siècle aux États-Unis (Binney, 1842) et n'était retrouvé au Québec presque uniquement à Gaspé et dans le Témiscamingue il y a 50 ans (Chichester et Getz, 1969). On le retrouve maintenant sur une grande partie du territoire, dont les forêts feuillues et boréales de l'est du Canada (L'Heureux et Angers, 2018 ; Moss et Hermanutz, 2010). Aucune étude ne s'est toutefois intéressée aux mécanismes impliqués dans son succès d'envahissement.

Depuis le 19e siècle, les écosystèmes forestiers sont de plus en plus perturbés par l'exploitation forestière (Wynn, 2017). Dans plusieurs régions du Canada, les coupes forestières sont devenues plus fréquentes que certaines perturbations naturelles, telles que les feux ou les épidémies d'insectes (Cyr *et al.*, 2009). L'exploitation forestière peut affecter la composition ou à la structure de l'habitat, en modifiant la diversité et la composition des espèces d'arbres (Clark et Covey, 2012) et de sous-étage (Götmark *et al.*, 2005 ; Macdonald et Fenniak, 2007 ; Roberts et Zhu, 2002), ainsi que la quantité de débris ligneux au sol (Angers *et al.*, 2005 ; Siitonen *et al.*, 2000). L'abondance de nombreuses espèces de gastéropodes, comme par exemple les limaces, dépend de ces attributs de l'habitat (Beyer et Saari, 1977, 1978 ; Johnston *et al.*, 2018 ; Kappes, 2005, 2006 ; Müller *et al.*, 2005 ; O'Hanlon *et al.*, 2020). La plupart des coupes forestières entraînent également une ouverture de la canopée pouvant causer une augmentation des températures et une diminution de l'humidité du sol (p. ex. Chen *et al.*, 1993 ; Heithecker et Halpern, 2006), deux attributs clés affectant l'aptitude phénotypique des limaces ainsi que leur comportement (Dainton et Wright, 1985 ; Kozłowski, 2009 ; Slotsbo *et al.*, 2013 ; Willis *et al.*, 2008). Il est difficile de déterminer si les habitats perturbés par des coupes seront plus ou moins favorables pour les différentes espèces de limaces comparativement aux habitats non perturbés car toutes les espèces ne répondent pas de la même manière aux changements d'attributs de l'habitat (Kappes, 2006). Les limaces ayant toutefois une très faible capacité de déplacement, des comportements avantageux ou une plasticité phénotypique importante devraient être des mécanismes prépondérants par lesquels elles font face aux perturbations.

En particulier, la compétition par interférence aurait pu favoriser le succès d'envahissement d'*A. subfuscus* s.l. En effet, ce complexe d'espèces est très agressif envers ses congénères et les autres espèces de limaces et peut parfois attaquer tous les individus qu'il rencontre (Rollo et Wellington, 1979). Il pourrait ainsi menacer le maintien des populations indigènes de limaces, comme par exemple celles du genre *Philomycus*, telle que *P. carolinianus*. Cette dernière a été désignée comme menacée en 2019 par le Comité sur la situation des espèces en péril au Canada (COSEWIC, 2019). *A. subfuscus* s.l. et les espèces du genre *Philomycus* apparaissent souvent conjointement dans les forêts d'Amérique du Nord (Chichester et Getz, 1969 ; Paustian, 2010) et consomment ou utilisent des ressources et microhabitats semblables (Paustian et Barbosa, 2012). Bien que la présence de compétition entre ces espèces ne soit pas clairement établie (Paustian et Barbosa, 2012), la compétition par interférence pour les refuges ou la nourriture est commune chez les gastéropodes. Elle peut être directe par le biais d'agressions (Kimura et Chiba, 2010 ; Rollo et Wellington, 1979), ou indirecte par le biais du mucus (Cameron et Carter, 1979 ; O'Hanlon *et al.*, 2020). *A. subfuscus* s.l. (*Arion* dans la suite du document) et les limaces indigènes du genre *Philomycus* (*Philomycus* dans la suite du document) sont donc de bons modèles biologiques pour déterminer (1) si les perturbations anthropiques (c.-à-d. coupes forestières) favorisent le succès d'envahissement des espèces animales exotiques (*Arion* dans le cas présent), (2) par quels mécanismes les espèces exotiques (*Arion*) profitent de la perturbation, et (3) si la compétition avec les espèces exotiques (*Arion*) peut représenter une menace pour le maintien des espèces indigènes (*Philomycus*).

Dans un premier chapitre, j'ai testé l'hypothèse de la perturbation selon laquelle la perturbation favorise le succès d'envahissement des espèces exotiques. Pour cela, j'ai évalué l'effet de l'occurrence d'une perturbation (c.-à-d., coupe forestière), son intensité et le temps depuis son occurrence sur l'abondance d'*Arion*, un indicateur du succès d'envahissement (Nordheimer et Jeschke, 2018). Pour mener à bien cet objectif, j'ai bénéficié de données d'études passées et de données récoltées spécifiquement pour cette thèse. Plus de 70 peuplements forestiers non perturbés ou perturbés par des coupes forestières ont été échantillonnés dans trois écosystèmes forestiers de l'est du Canada. Les peuplements coupés différaient en termes d'intensité de coupe (retrait partiel à total des arbres vivants et de la biomasse résiduelle) et temps écoulé depuis la coupe (1 à 66 ans).

Dans un second temps, j'ai cherché à identifier les mécanismes associés au succès d'envahissement d'*Arion* dans les habitats perturbés. Plus particulièrement, j'ai évalué (i) le rôle des modifications d'attributs de l'habitat engendrées par la coupe forestière (chapitre II), (ii) des valeurs de traits comportementaux, (iii) de la plasticité comportementale et (iv) de la compétition interspécifique par interférence dans son succès d'envahissement (chapitre III). J'ai notamment réalisé des expériences en milieu contrôlé (chapitre III) afin de déterminer si *Arion* avait des valeurs de traits comportementaux plus avantageuses (hypothèse de l'envahisseur idéal) et une plus grande plasticité comportementale que *Philomycus* (hypothèse de la plasticité) en réponse à une diminution de l'humidité du sol (simulant l'effet d'une coupe forestière). Je me suis intéressée à l'activité exploratoire et à l'audace (*boldness* en anglais), deux comportements pouvant influencer le succès d'envahissement des espèces exotiques animales (Chapple *et al.*, 2012).

Dans un dernier temps, j'ai évalué si les coupes forestières pouvaient promouvoir le déclin de *Philomycus*, et quand c'était le cas, j'ai évalué le rôle de la modification des attributs de l'habitat (chapitre II) et de la compétition par interférence avec *Arion* dans ce déclin (chapitre III). La présence potentielle de compétition par interférence a été testée en milieu contrôlé, en évaluant si la présence d'*Arion* affectait le comportement de *Philomycus* (déplacement, repos, alimentation, et utilisation des refuges) et vice-versa.

CHAPITRE I

TOWARDS A BETTER UNDERSTANDING OF THE EFFECT OF ANTHROPOGENIC HABITAT DISTURBANCE ON THE INVASION SUCCESS OF ALIEN SPECIES

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1.1 Résumé

L’hypothèse de la perturbation propose qu’une perturbation de l’habitat favorise le succès d’envahissement des espèces exotiques. Cette formulation manquant de spécificité, la communauté scientifique a souvent étudié indépendamment l’effet de l’occurrence d’une perturbation et celui de ses caractéristiques (p. ex. son intensité) sur le succès d’envahissement des espèces exotiques. Cependant, cette hypothèse ne permet pas de formuler de prédictions spécifiques concernant ces deux effets de la perturbation, ce qui pourrait expliquer pourquoi elle n’est pas toujours soutenue. L’objectif de cette étude était de déterminer les effets de l’occurrence d’une perturbation anthropique (c.-à-d. coupe forestière), de son intensité et du temps écoulé depuis son occurrence sur le succès d’envahissement (c.-à-d. l’abondance) d’*Arion subfuscus* s.l., un complexe envahissant composé de deux espèces de limaces exotiques originaires d’Europe. Nous avons disposé des pièges fosses dans la forêt boréale et tempérée de l’Est du Canada dans des peuplements témoins et des peuplements perturbés par des coupes forestières. Ces derniers variaient en termes d’intensité de la récolte (retrait partiel à complet des arbres vivants et de la biomasse résiduelle) et le temps écoulé depuis la coupe (de 1 à 66 ans). Nos résultats n’ont révélé aucun effet positif de l’occurrence de la coupe forestière sur l’abondance d’*A. subfuscus* s.l., mais ont montré que son succès d’envahissement était influencé par l’intensité de la récolte et le temps écoulé depuis celle-ci. Nous avons ainsi proposé un cadre conceptuel de l’hypothèse de la perturbation qui prend explicitement en compte l’effet de l’intensité de la perturbation et du temps écoulé depuis son occurrence sur le succès d’envahissement des espèces exotiques, incluant la manière dont ces deux caractéristiques affectent les conditions biotiques et abiotiques de l’écosystème. Ce cadre, qui peut être appliqué aux espèces exotiques animales et végétales, permet de déterminer plus précisément dans quelles circonstances une perturbation de l’habitat va favoriser le succès d’envahissement des espèces exotiques.

Mots clés : Hypothèse de la perturbation**,** perturbation de l’habitat, espèce exotique, succès d’envahissement, coupe forestière, limace

1.2 Abstract

The disturbance hypothesis postulates that habitat disturbance favours the invasion success of alien species. Its unspecific formulation has led invasion biologists to evaluate either the effect of the occurrence of a disturbance or its characteristics (e.g., its intensity) on the invasion success of alien species. However, this hypothesis is unclear about these two effects, which might explain why studies offer an ambivalent support to this hypothesis. Our objective was to determine the effects of the occurrence of an anthropogenic disturbance (i.e., logging), its intensity, and the time since its occurrence on the invasion success (i.e., abundance) of an alien slug species complex, *Arion subfuscus* s.l. We used pitfall trapping in stands located in boreal and temperate forest ecosystems in eastern Canada. We sampled control and logged stands that differ in harvesting intensity (from partial to complete removal of standing live trees and downed biomass) and time since logging (from 1 to 66 years). Our results did not reveal any significant positive effects of logging occurrence on *A. subfuscus* s.l. abundance and showed that its invasion success was influenced by the logging intensity and the time-since-logging. We thus propose a conceptual framework of the disturbance hypothesis that explicitly accounts for the disturbance intensity and time since its occurrence, including the way they alter the biotic and abiotic conditions of the ecosystem. This framework, which can be applied to alien animals and plants, provides specific predictions on the conditions under which habitat disturbance promotes the invasion success of alien species.

Keywords: Disturbance hypothesis, habitat disturbance, alien species, invasion success, logging, slug

1.3 Introduction

Humans have introduced, both accidentally or intentionally, many species outside of their native ranges (i.e., alien species), but only some of these will become invasive by increasing in abundance and spreading from the area of introduction (Blackburn *et al.*, 2011 ; Williamson and Fitter, 1996). Understanding the mechanisms affecting the successful establishment, dominance, and spread ("invasion success") of alien species is central to predicting future biological invasions.

Anthropogenic habitat disturbance can increase the vulnerability of an ecosystem to biological invasions by modifying its biotic and abiotic conditions (Catford *et al.*, 2009 ; Colautti *et al.*, 2006b ; Lonsdale, 1999). Invasion biologists have thus postulated that habitat disturbance favours the invasion success of alien species, a formulation known as the disturbance hypothesis (Elton, 1958 ; Hobbs and Huenneke, 1992). The idea underlying this hypothesis is that native species are better adapted to pre-disturbance conditions than are alien species (Nordheimer and Jeschke, 2018). Consequently, any disturbance that modifies biotic and abiotic conditions could favour alien species at the expense of native species. This might be possible if disturbance alters habitat attributes (i.e., abiotic and vegetation characteristics), such that the fitness (i.e., survival and reproduction) of native species is decreased, as is their ability to take up resources. The latter effect increases the quantity of resources that are made available to alien species through reduced interspecific interactions (i.e., competition) (Davis *et al.*, 2000). Habitat disturbance could likewise create opportunities for alien species invasions by providing suitable habitat attributes for their establishment and spread (Hobbs and Huenneke, 1992 ; Ning *et al.*, 2019).

The disturbance hypothesis has been mainly tested with alien plants and its support is equivocal (Lozon and MacIsaac, 1997 ; Nordheimer and Jeschke, 2018). The meta-analysis that was conducted by Nordheimer and Jeschke (2018) revealed that half of the studies on the success of alien species reported a positive relationship between disturbance and invasion success, thereby supporting the disturbance hypothesis, whereas the others either indicated a negative relationship or were inconclusive. This inconsistency among results might be due to the lack of specificity in the formulation of the disturbance hypothesis, which leads invasion biologists to evaluate either the effect of the occurrence of a disturbance (e.g., changes in cover or abundance of alien species between disturbed and undisturbed habitats; Callaham Jr *et al.*, 2003 ; Lake and Leishman, 2004 ; Malumbres-Olarte *et al.*, 2014) or the effect of its characteristics (e.g., changes in cover, abundance or occurrence of alien species between different levels of habitat disturbance; Altman and Whitlatch, 2007 ; Grez *et al.*, 2013). These two distinct dimensions of the disturbance hypothesis may lead to different results with respect to the response of alien species. Therefore, the conditions underlying the invasion success of alien species in disturbed ecosystems could be made more explicit by a closer examination of the characteristics of habitat disturbance, and how they modify the biotic and abiotic conditions of an ecosystem. A more specific formulation of the disturbance hypothesis is thus essential to make more accurate predictions about the effect of habitat disturbance on the invasion success of alien species.

Since the 19th century, forest ecosystems in North America have been increasingly disturbed by commercial harvesting (Wynn, 2017). In several geographic regions, harvesting has now replaced natural disturbances such as wildfires and insect outbreaks as the primary disturbance (Cyr *et al.*, 2009). To our knowledge, only a few studies have specifically examined the effects of tree harvesting on the invasion success of alien animals which makes it difficult to draw general conclusions about the effect of logging on animal invasions. These studies reported that the invasion success of alien animal species (vertebrates and invertebrates) can be favoured by tree harvesting, with the alien species being more abundant in logged than in unlogged forests (e.g., Balete *et al.*, 2009 ; Rodriguez-Cabal *et al.*, 2015 ; Wearn *et al.*, 2017 ; Zettler *et al.*, 2004) or more abundant in more intensively than in less intensively logged forests (e.g., Kappes, 2006 ; Rickart *et al.*, 2011 ; Todd *et al.*, 2008).

Half of the species of slugs (Gastropoda, Pulmonata) that are found in Canada are not native (Grimm *et al.*, 2009). Among these, *Arion subfuscus* (Draparnaud, 1805) sensu lato is a species complex that is composed of *Arion subfuscus* (Draparnaud, 1805) sensu stricto and *Arion fuscus* (Müller, 1774). These two species are native to Europe (L'Heureux and Angers, 2018 ; Pinceel *et al.*, 2005). How and when these species were introduced into Canada remains unclear. Nevertheless, *Arion subfuscus* s.l. has rapidly expanded its distribution in eastern Canada. Fifty years ago, the species complex was only located in a few areas of Quebec (Chichester and Getz, 1969), but it is now widespread across eastern Canada ecosystems, including forests (L'Heureux and Angers, 2018). In southern Quebec, the two *A. subfuscus* s.l. species are present, but *Arion fuscus* is probably much more abundant than *A. subfuscus* s.str. (L'Heureux and Angers, 2018). Slug communities are understudied in eastern Canadian forest ecosystems, despite their roles in litter decomposition (Jennings and Barkham, 1979) and their importance in the food web structure of the soil (Laigle *et al.*, *submitted*). The processes underlying the successful invasion of *A. subfuscus* s.l. into forest ecosystems are unclear. However, studies suggest that alien slugs are less sensitive to disturbance than are native slug species (Ryser *et al.*, 2011) and that habitat disturbance, such as forest management practices, may favour their invasion success, e.g., abundance (Kappes, 2006 ; Kappes and Schilthuizen, 2014). *A. subfuscus* s.l. thus represents a suitable biological model to test the disturbance hypothesis.

The goal of this study was to determine the overall effects of a disturbance, i.e., logging (objective 1), its intensity (objective 2), and time since its occurrence (objective 3), on the abundance (i.e., a measure of invasion success, Nordheimer and Jeschke, 2018) of the invasive alien slug species complex *A. subfuscus* s.l. (hereafter, *Arion*). Consistent with the disturbance hypothesis, we predicted that *Arion* abundance would be higher in logged than in unlogged mature forests (objective 1). Slugs are highly sensitive to variation in habitat attributes, such as temperature (Clemente *et al.*, 2008 ; Kozłowski, 2009 ; Slotsbo *et al.*, 2013 ; Udaka and Numata, 2008 ; Willis *et al.*, 2008) and soil moisture (Willis *et al.*, 2008 ; Young and Port, 1991), and the abundance of gastropods is influenced by the quantity of coarse woody debris (Kappes, 2005). Intense logging practices could modify these habitat attributes so drastically that they would become unsuitable for both alien and native slugs. Accordingly, we can expect intensively logged forests to be less suitable for hygrophilous species (inhabiting moist habitats), such as slugs, given that canopy closure, soil moisture and the quantity of coarse woody debris are low because of extensive removal of live tree and downed biomass volumes. We further predicted that increasing logging intensity would increase *Arion* abundance until a tipping point (threshold) was reached, beyond which changes in habitat attributes would not favour *Arion* survival and ultimately its invasion success (objective 2). We also predicted that *Arion* abundance would increase with time-since-logging, and given enough time, would stabilise once the establishment phase is completed and habitat saturation is reached (objective 3). In light of our results, we have proposed a more specific formulation of the disturbance hypothesis through a conceptual framework.

1.4 Materials and methods

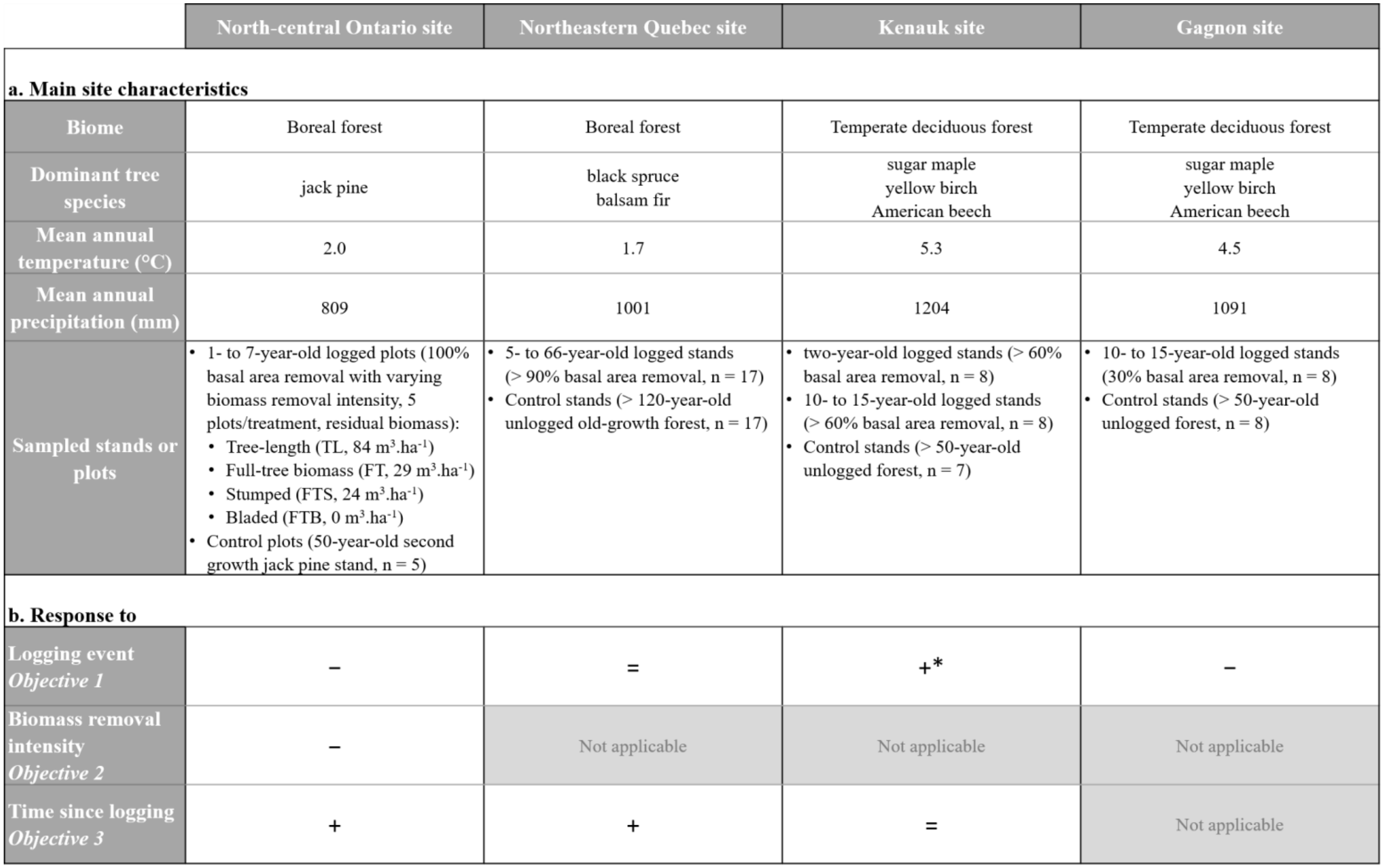
1.4.1 Study sites

We took advantage of previous and ongoing studies in four sites located in three forest ecosystems in eastern Canada. Two sites are situated in the boreal forest: the first one is in north-central Ontario (hereafter, north-central Ontario site: 47°42’ N, 83°36’ W), and the second one is in northeastern Quebec (hereafter, northeastern Quebec site, 49°35’ N, 68°21’ W; Figure S1.1). The third and fourth sites are located in temperate forests of southern Quebec in the Kenauk nature reserve (45°42’ N, 74°53’ W;

hereafter, Kenauk site), and near Gagnon Lake (46°07’ N, 75°09’ W; hereafter, Gagnon site; Figure S1.1).

These sites differed in terms of their dominant tree species and climate (Table 1.1a). The coniferous forest in the north-central Ontario site is dominated by jack pine (*Pinus banksiana* Lambert), whereas the canopy cover in the northeastern Quebec site consists of black spruce (*Picea mariana* (Miller) B.S.P.) in association with balsam fir (*Abies balsamea* (L.) Miller). Deciduous forest at the Gagnon and Kenauk sites is dominated by sugar maple (*Acer saccharum* Marshall), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrhart) (Nolet *et al.*, 2015) (Table 1.1a). Mean annual temperature (1981–2010) is lower at sites located in the boreal forest compared to sites in the temperate forest (Table 1.1a). Mean annual precipitation (1981–2010) is the lowest in north-central Ontario, intermediate in the northeastern Quebec and Gagnon sites, and the highest in the Kenauk site (Environment Canada 2020, Table 1.1a).

Table 1.1a: Summary of the main characteristics (i.e., vegetation, climate, and logging treatments) of the four study sites. Climate data were obtained from Environment Canada (2020). b: Summary of the responses of the abundance of the invasive alien slug species complex *A. subfuscus* s.l. to a logging event, to its intensity and to the time since logging in the four study sites. The + and – signs indicate a positive (increased abundance) or a negative (decreased abundance) response to logging, respectively. * indicates a marginally significant effect



	North-central Ontario site	Northeastern Quebec site	Kenauk site	Gagnon site
a. Main site characteristics				
Biome	Boreal forest	Boreal forest	Temperate deciduous forest	Temperate deciduous forest
Dominant tree species	jack pine	black spruce balsam fir	sugar maple yellow birch American beech	sugar maple yellow birch American beech
Mean annual temperature (°C)	2.0	1.7	5.3	4.5
Mean annual precipitation (mm)	809	1001	1204	1091
Sampled stands or plots	• 1- to 7-year-old logged plots (100% basal area removal with varying biomass removal intensity, 5 plots/treatment, residual biomass): • Tree-length (TL, 84 m^3.ha^{-1}) • Full-tree biomass (FT, 29 m^3.ha^{-1}) • Stumped (FTS, 24 m^3.ha^{-1}) • Bladed (FTB, 0 m^3.ha^{-1}) • Control plots (50-year-old second growth jack pine stand, n = 5)	• 5- to 66-year-old logged stands (> 90% basal area removal, n = 17) • Control stands (> 120-year-old unlogged old-growth forest, n = 17)	• two-year-old logged stands (> 60% basal area removal, n = 8) • 10- to 15-year-old logged stands (> 60% basal area removal, n = 8) • Control stands (> 50-year-old unlogged forest, n = 7)	• 10- to 15-year-old logged stands (30% basal area removal, n = 8) • Control stands (> 50-year-old unlogged forest, n = 8)
b. Response to				
Logging event ***Objective 1***	–	=	+*	–
Biomass removal intensity ***Objective 2***	–	Not applicable	Not applicable	Not applicable
Time since logging ***Objective 3***	+	+	=	Not applicable

1.4.2 Experimental design and slug sampling

North-central Ontario site–To address our three objectives, we took advantage of the Island Lake Biomass Harvest Experiment (Kwiaton *et al.*, 2014). This experiment took place in a second-growth jack pine stand that was originally clear-cut in 1959. The site was scarified and hand-seeded in 1960, but due to poor initial regeneration, it was replanted with jack pine in 1962. Part of the site was then clear-cut harvested during winter 2010–2011, and implementation of a gradient of biomass removal and forest floor treatment following clear-cutting allowed to study the effects of biomass removal intensity on biodiversity and forest productivity. From the least to the most intense, the treatments were: (1) tree-length harvest (TL), where boles were delimbed, cut at 10 cm diameter and removed, while residual slash was distributed evenly throughout the treatment using an excavator; (2) full-tree biomass harvest (FT), where boles with branches were removed and delimbed outside the experimental plots; (3) stump removal (FTS), where boles and branches were removed as in FT, while stumps with large attached roots were removed and placed at least 10 m beyond the experimental plots; and (4) blading (FTB), where boles, branches, and stumps were removed as in FTS and where roots, woody debris and the upper 5 cm of the mineral soil were removed with an excavator fitted with large metal blades. The TL, FT, and FTS plots were scarified using disc trenching with 2.1 m spacing between trench centres. These treatments were set up to assess the outcome of an increase in biomass removal on biodiversity since logging residues could be an important source of raw material for bioenergy production in Canada. Although the most intense treatment is an unusual sylvicultural practice, forest residual biomass is often removed before the establishment of plantations. Each treatment (TL, FT, FTS, FTB) was replicated in five blocks (i.e., a total of five plots per treatment; Figure S1.2). Each plot measured 70 × 70 m and was separated from one another by at least 25 m. This distance should be sufficient to achieve the independence in sampling *Arion* abundance among plots; slug home range for individuals with larger body size (7–15 cm) cover a 7.6-metre diameter circle (Grimm and Paill, 2001). Plots were divided into four 35 × 35 m subplots, and the two western subplots were hand-sprayed in August 2011 with glyphosate herbicide to control vegetation. Although herbicide application decreased over time in Canada, it is an effective management technique and is still applied to release of high-value conifers for competing vegetation. The two northern and southern subplots were replanted respectively with jack pine and black spruce in 2012 following conventional site preparation (mechanical disk trenching) (Figure S1.2; for further details, see Kwiaton *et al.*, 2014). To evaluate the effect of logging on *Arion* abundance (objective 1), five plots (70 × 70 m), that were separated by 20 m from one another and by 50 m from the logged forest to minimise edge effects, were sampled in an adjacent 8-ha forest stand, as a control treatment for the gradient of biomass removal treatments (Figure S1.2). These control plots have the same origin as the biomass removal plots (i.e., clear-cut harvested and planted with jack pine in 1962), but they were not logged in 2011 (i.e., no clear-cut harvesting, downed biomass removal and planting). Differences of *Arion* abundance between these control plots and biomass removal plots should be mainly the result of logging in 2011. *Arion* abundance in control plots, however, may not reflect its population size in unlogged forests of the area.

In this study, we used pitfall traps a common method to collect terrestrial invertebrates, such as slugs (Nystrand and Granström, 2000 ; Pigot and Leather, 2008 ; Rodriguez-Cabal *et al.*, 2015). As other surface traps, it may underestimate densities of slugs in the habitats while capturing spatial patterns in their abundances (Archard *et al.*, 2004). Slugs were collected in each plot (n = 25) with eight pitfall traps (i.e., two per subplot, for a total of 200 pitfall traps) every 7 to 16 days from May to August 2012 and 2013. This sampling was repeated in 2018 to determine the effect of time-since-logging with biomass removal on *Arion* abundance (objective 3) over a short time-scale. Pitfall traps were filled with 150 mL of propylene glycol as a preservative, 150 mL of water, and a small amount of detergent to break the surface tension. For this study, we only used slug counts from the two non-herbicide subplots (i.e., data from four of the eight pitfall traps per biomass removal plots were not used; Figure S1.2); we did not know whether the herbicide application would exert direct or indirect effects on *Arion* abundance. To standardise sampling effort between the plot types, we only used four of eight pitfall traps per control plot (i.e., the eastern pitfall traps).

Northeastern Quebec site–To evaluate the overall effect of logging (objective 1) and time- since-logging (objective 3) on *Arion* abundance, we took advantage of a previous study focusing on the effects of clear-cutting on animal biodiversity. A chronosequence approach was used to determine how bird, small mammal, and invertebrate (including slugs) communities change during post-logging forest succession (for details, see: Dupuch and Fortin, 2013 ; Le Borgne *et al.*, 2018b). We sampled paired stands (patch of trees uniform in terms of composition and structure) consisting of a 5- to 66-year-old clear-cut stand (n = 17) that was adjacent to a control stand (n = 17; Figure S1.3). The latter was an unlogged old-growth forest > 120 years of age, while > 90% of basal area was removed in the clear-cut stands, with a high level of forest floor disturbance because of heavy machinery traffic. The paired stands shared a boundary ≥ 250 m long, and each stand (logged or control) covered an area of at least 200 × 250 m (> 5 ha). We selected the pairs of stands according to three criteria: (1) stand structure and composition (i.e., dominated by black spruce) within the old-growth forest was similar among stands (i.e., dominated by black spruce with equivalent basal area et volume of coarse woody debris); (2) regeneration in logged stands consisted of conifers (black spruce and balsam fir); and (3) streams and roads were absent in both paired stands.

Slugs were collected in each stand (n = 34) with 10 pitfall traps installed for a single 10 to 12-day period between June and September 2011. Pitfall traps were positioned along a transect that ran perpendicular to and across the centre of the logged and control stands. From the shared boundary of the paired stands, we installed pitfall traps at 5 m intervals for the first five traps, at 10 m intervals for the four following traps, and 20 m for the last traps, which were located towards the ends of the transect (Figure S1.3). Each pitfall trap was filled with a solution of 40% ethanol with trace quantities of 5% acetic acid to kill and preserve individuals. Acetic acid was used to keep the specimen flexible.

Southern Quebec sites− The study in the temperate forest of southern Quebec was conducted in the Kenauk and Gagnon sites and was specifically designed to evaluate the overall effects of logging (objective 1, Kenauk and Gagnon sites) and time-since-logging (objective 3, Kenauk site) on *Arion* abundance. At the Kenauk site, we sampled two-year-old logged stands (n = 8), 10- to 15-year-old logged stands (n = 8), and control stands (n = 7, > 50-year-old uneven-aged stands without any sign of recent or old logging activities; Figure S1.4). The two-year-old stands originated from shelterwood cutting in 2014–2015, whereas the 10- to 15-year-old stands had been clear-cut between 1999 and 2004. These two treatments removed more than 60% of the basal area and were separated from one another by > 80 m. At the Gagnon site, we sampled 10- to 15-year-old stands (n = 8) that were harvested by selection cutting (i.e., 30% basal area removal) in 2006 and control stands (n = 8) that were located in old uneven-aged stands without any sign or record of logging activities (Figure S1.4). Slugs were collected in each stand with four pitfall traps every 9 to 25-days between July and September 2016. Pitfall traps were installed in each cardinal direction (N, S, E, and W), spaced about 20 m apart, and filled with 100 mL of 40% ethanol (as a preservative) with trace quantities of 5% acetic acid.

For the four sites, slugs were preserved in 70 to 100% ethanol solutions and identified to species (*Arion subfuscus* s.l., *Pallifera dorsalis* [Binney, 1842], *Deroceras laeve* [Müller, 1774]) or to genus (*Philomycus* spp.), based upon external morphological characters (Grimm *et al.*, 2009) or dissection of the genitalia (Pinceel *et al.*, 2004), together with a few genetic analyses. Fragments of the mitochondrial DNA COI gene were sequenced by the Canadian Centre for DNA barcoding (CCDB, http://www.ccdb.ca/) and Genome Quebec (https://www.genomequebec.com/) through the Barcode of Life Data Systems (BOLD, http://www.boldsystems.org/; Ratnasingham and Hebert, 2007). Voucher specimens are preserved at the Institut des Sciences de la Forêt Tempérée (Ripon, QC, Canada) and at the Great Lakes Forestry Centre (Sault Ste Marie, ON, Canada).

The number of *Arion* that were collected in pitfall traps was summed at the stand level for the southern Quebec and northeastern Quebec sites, and at the plot by sampling year level for the north-central Ontario site. Data from pitfall traps that were disturbed by fauna were not included in the study (< 3% in all sites, except for Kenauk, where it was 20%).

1.4.3 Statistical analysis

For each of the three objectives, we modelled *Arion* abundance (number of individuals per stand or plot) with generalised linear mixed models (GLMM) with a negative binomial distribution, which is adapted for over-dispersed count data. The number of trap nights per stand or plot was log-transformed and included in the analyses as an offset variable to adjust models for differences in sampling effort among stands or plots. The offset variable makes model adjustments with its regression coefficient being fixed at 1 (Hilbe, 2007). All analyses were carried out in R v.3.6.3 (R Core Team, 2020) with the package *glmmTMB* (Brooks *et al.*, 2017), *emmeans* (Lenth, 2020) and *ARTool* (Wobbrock *et al.*, 2011).

Objective 1−To determine the overall effect of logging on the invasion success of *Arion*, we compared its abundance between logged and control stands or plots in the four sites (Gagnon site, n = 16; Kenauk site, n = 23; northeastern Quebec site, n = 34; and north-central Ontario site, n = 75) by including stand or plot type as a fixed effect (binary variable: logged vs control) in the GLMMs.

Objective 2−We determined the effect of biomass removal intensity on *Arion* abundance at the north-central Ontario site (n = 60) by including the biomass removal treatment intensity as a fixed effect (four-level categorical variable: TL, FT, FTS, FTB). Multiple comparison tests among the four biomass removal intensities were performed using the estimated marginal means and Holm-Bonferroni correction (Lenth, 2020) to determine which mean abundances of *Arion* significantly differed from one another.

Objective 3−To test the effect of time-since-logging on *Arion* abundance, we included a two-level categorical variable (2 years vs 10- to 15-years; Kenauk site, n = 16) or a log-transformed continuous variable (ranging from 5- to 66-years; northeastern Quebec site, n = 17) as a fixed effect. At the north-central Ontario site (n = 60), given the short duration of the study (7 years post-logging), habitat attributes that are suitable for *Arion* may recover faster in the less intense treatments than in the most intense. Therefore, we included time-since-logging (three-level categorical variable: 1, 2, and 7 years), biomass removal intensity (four-level categorical variable: TL, FT, FTS, FTB) and their interaction as fixed effects in the model to determine if the increase of *Arion* abundance with time-since-logging would have been higher in the less intense compared to the most intense treatments. Due to problems in the estimation of few variable coefficients in this analysis based upon a negative binomial distribution, we used a non parametric analysis of variance on adjusted rank transformed *Arion* abundances (Leys and Schumann, 2010) that were corrected for differences in sampling effort (i.e., abundance per plot divided by the number of trap nights per plot). We then conducted multiple comparison tests with the bladed biomass removal treatment in the first year after biomass removal (i.e., 2012) as reference levels using the estimated marginal means and Holm-Bonferroni correction (Lenth, 2020).

For all analyses that were based upon the north-central Ontario data, we included sampling year (except for objective 3, where it was included as a fixed effect) and block as crossed random effects to account for differences in environmental conditions (e.g., precipitation and air temperature) among the three sampling years and the lack of independence arising from repeated observations within blocks. For the analysis based upon northeastern Quebec data, we included each pair of stands as a random effect in the models to account for the non-independence of data.

1.5 Results

Across the four sites, we captured 6176 slugs, which could be classed into at least four species. *Arion subfuscus* s.l. were the most frequently collected species (96.7% of all catches) (Table S1.1). The other species that were collected were native to North America and included *Deroceras laeve*, *Pallifera dorsalis*, and philomycid slugs (*Philomycus* spp.) (Table S1.1). *Deroceras laeve* was frequently collected in the northeastern Quebec site (44.4% of the catches), while it was rarely present in the north-central Ontario and the southern Quebec sites. Few *Pallifera dorsalis* were collected in the north-central Ontario and the southern Quebec sites, while *Philomycus* spp. was only present in the southern Quebec sites. We collected *Arion subfuscus* s.l. in nearly all stands or plots (from 80% to 100%) at the Gagnon and the north-central Ontario sites, but only 57% to 75% in those plots at the northeastern Quebec and Kenauk sites (Table S1.1).

1.5.1 Overall effect of logging on *Arion* abundance (objective 1)

Although the effect of logging occurrence on *Arion* abundance varied among the different forest ecosystems, this factor did not benefit its invasion success on any site. Indeed, *Arion* abundance tended to be higher in logged than in control stands only at the Kenauk site ($\beta \pm SE$: 1.04 ± 0.56, $P = 0.064$; Figure 1.1), whereas it was significantly lower in logged than in control plots or stands at the north-central Ontario ($\beta \pm SE$: -2.02 ± 0.58, $P < 0.001$, Figure 1.1) and Gagnon sites ($\beta \pm SE$: -0.70 ± 0.35, P

= 0.048; Figure 1.1). *Arion* abundance was similar in logged and control stands in the northeastern Quebec site (β ± SE: 0.41 ± 0.27, P = 0.127; Figure 1.1).

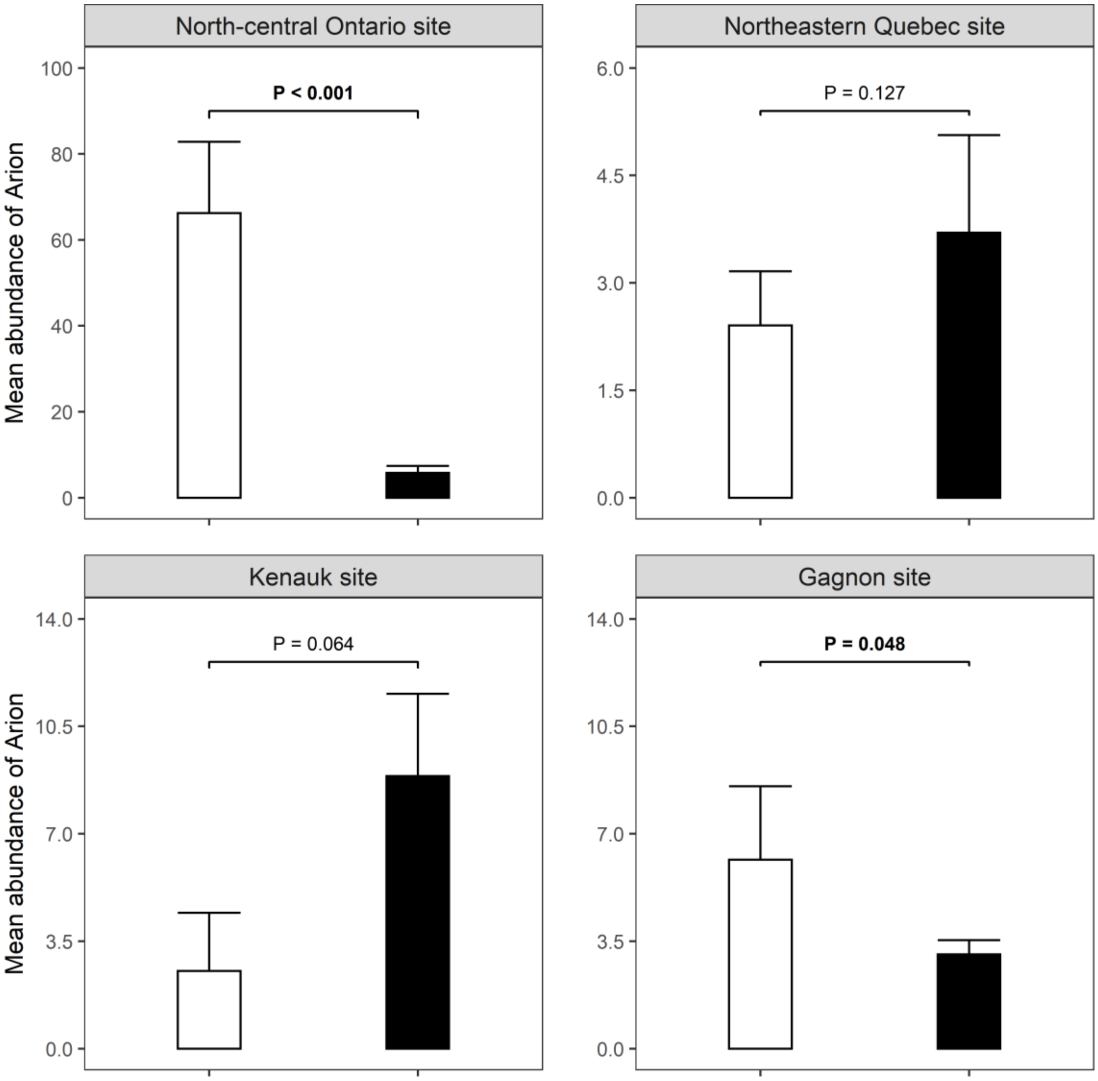


Figure 1.1: Mean abundance of *Arion* (slugs.100 trap nights^{-1}) in control (white bar) and logged stands or plots (black bar) in the boreal forest of the north-central Ontario site (the logged plot category includes the four biomass removal treatments) and the northeastern Quebec site, and in the temperate forest of the Kenauk and Gagnon sites. The mean abundance of *Arion* in the north-central Ontario site has been estimated from the three sampling year data. Bold type indicates a significant difference in *Arion* abundance between stand or plot types. See Table 1.1a for a description of control and logged stands or plots in each site

1.5.2 Effect of biomass removal intensity and time-since-logging on *Arion* abundance (objectives 2 and 3)

At the north-central Ontario site, *Arion* abundance significantly decreased with increasing intensity of biomass removal (Figure 1.2). Similar to the effect of logging occurrence, the effect of time-since-logging on *Arion* abundance varied among the sites. At the north-central Ontario site, *Arion* abundance increased with time-since-logging, especially in plots with the lowest biomass removal intensities (i.e., TL; significant treatment x time-since-logging interaction; F = 4.109, P = 0.002; Figure 1.3a, Table S1.2). *Arion* abundance also increased with time-since-logging in the northeastern Quebec site (β ± SE: 1.56 ± 0.61, P = 0.010), with *Arion* being ultimately more abundant in 66-year-old logged stands than in the controls (Figure 1.3b). At Kenauk site, *Arion* abundance was similar in two-year-old and 10- to 15-year-old logged stands (β ± SE: 0.04 ± 0.51, P = 0.942; Figure 1.3c).

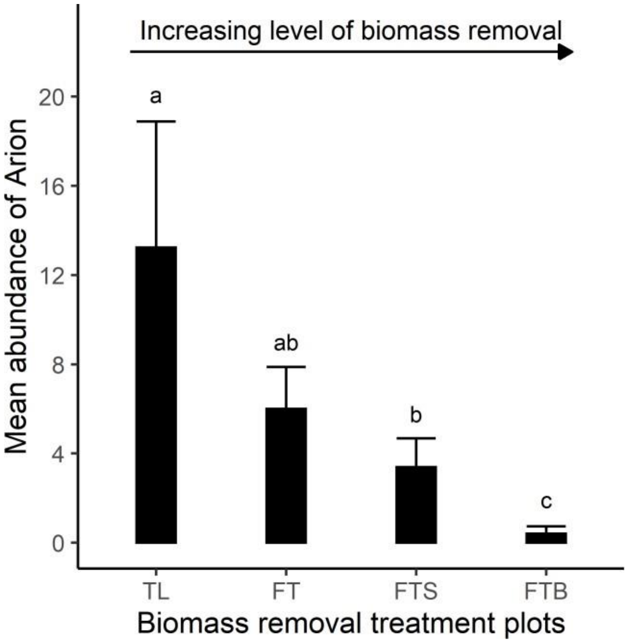


Figure 1.2: Mean abundance of *Arion* (slugs.100 trap nights^{-1}) per plot in the biomass removal treatment plots in the boreal forest of the north-central Ontario site, where TL: tree-length, FT: full-tree biomass, FTS: stumped, and FTB: bladed. The mean abundance of *Arion* has been estimated from the three sampling year data. Errors bars represent standard errors. Different letters indicate the significance of pairwise comparisons with a Holm-Bonferroni correction

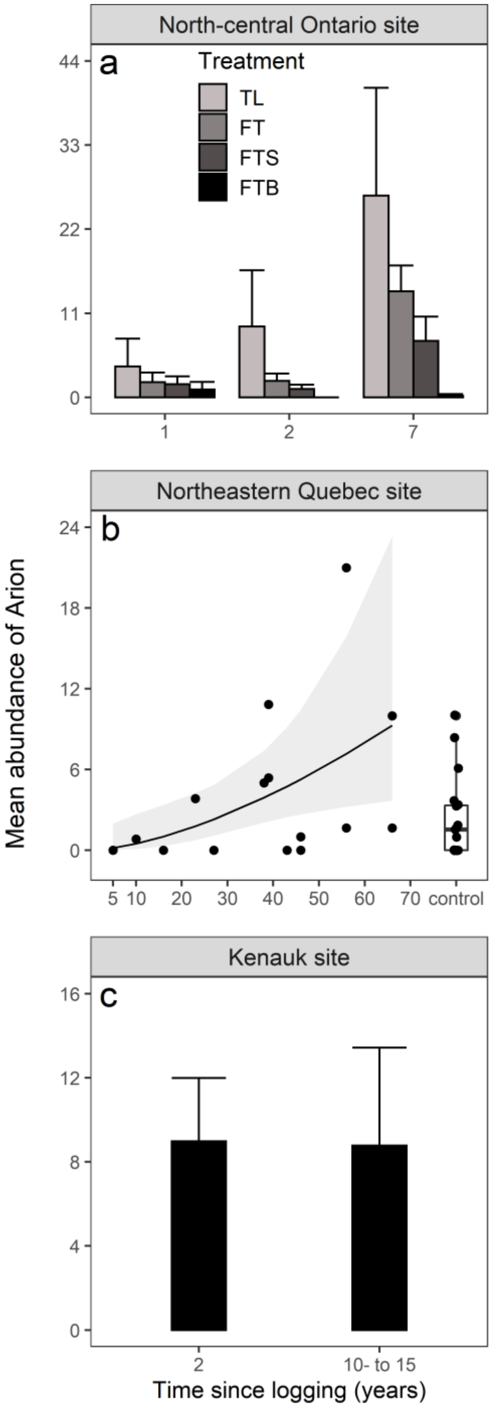


Figure 1.3: Mean abundance of *Arion* (slugs.100 trap nights^{-1}) in logged stands or plots: (a): 1, 2 and 7 years after logging at the north-central Ontario site (TL: tree- length; FT: full-tree biomass; FTS: stumped, FTB: bladed); (b) along a chronosequence ranging from 5- to 66-year-old and in the control stands at the northeastern Quebec site (the shaded area represents the 95% confidence interval around the fitted values, shown as a solid black line); (c) 2 years and 10- to 15 years after logging at the Kenauk site. Errors bars represent standard errors. Data at the Gagnon site are not shown since the logged stands did not differ in time since logging

1.6 Discussion

Our results provide partial support for the disturbance hypothesis (Elton, 1958 ; Hobbs and Huenneke, 1992). On the one hand, our results did not reveal any significant positive effects related to the occurrence of logging (Table 1.1b). The occurrence of a disturbance alone has little power to explain the invasion success of alien species, which is consistent with previous studies on alien plants (Jauni *et al.*, 2015 ; Moles *et al.*, 2012). On the other hand, *Arion* abundance usually increased with time-since-logging (Table 1.1b) and it can be more abundant in logged than in control stands given sufficient time for recovery. Thus, our results showed that the effect of logging on the invasion success of *Arion* can only be thoroughly understood when taking into account the characteristics of the disturbance (i.e., its intensity and time since its occurrence, Table 1.1b). Indeed, as previously stated by other invasion biologists, a disturbance would favour the invasion success of alien species only if it modifies the biotic and abiotic conditions of the recipient ecosystem in a manner that favours the establishment or spread of alien species (Hobbs and Huenneke, 1992 ; Lozon and MacIsaac, 1997). This statement thus implies that a disturbance, according to its characteristics, may not favour the invasion success of alien species. The disturbance hypothesis thus requires a more specific formulation to make more accurate predictions about the effect of habitat disturbance on the invasion success of alien species.

Arion subfuscus s.l. lives in a variety of habitats (e.g., woodlands, roadside margins, and fields; Chichester and Getz, 1969 ; Kappes and Schilthuizen, 2014 ; L'Heureux et Angers, 2018), which suggests that it can cope with a wide range of abiotic conditions. Yet, removing more downed biomass (i.e., increasing logging intensity) has been detrimental to its abundance (north-central Ontario site; Table 1.1b). Soil moisture content and woody debris are among key habitat attributes determining the presence and persistence of some terrestrial gastropods in forest. Soil moisture content influences egg-laying behaviours and the activity levels of slugs (Willis *et al.*, 2008 ;

Young and Port, 1991), and woody debris serves as micro-climatic refuges and oviposition sites (Harmon *et al.*, 1986 ; Kappes, 2005). In addition to the low soil moisture content resulting from the low canopy cover and retention of precipitation (high evaporative demand) (Venier *et al.*, 2017), the removal of most or all of the woody debris from the biomass removal treatments may have made the abiotic site conditions harsh enough to shift *Arion* away from its tolerance limits, induce stress and lead to decreased abundance (as is often observed in native animals: Burivalova *et al.*, 2015 ; Niemelä *et al.*, 2007 ; Vanderwel *et al.*, 2007). This explanation is consistent with the fact that unsuitable abiotic conditions are known to prevent alien animal and plant species from establishing and spreading or reduce their invasion success, (Gerhardt and Collinge, 2007 ; Hawes and Parrish, 2003 ; Menke *et al.*, 2007 ; Ning *et al.*, 2019 ; Warren II *et al.*, 2020).

As was the case for the high-intensity logging event, low-intensity logging events also could have negatively influenced the invasion success of alien species. Indeed, logging has been slightly detrimental to *Arion* abundance at the Gagnon site, even though the logging intensity was the lowest among our sites (only 30% of the standing basal area removed; Table 1.1b). In contrast to the north-central Ontario site (100% of the standing basal area removed, with or without downed biomass removal), the logged and control stands at the Gagnon site were similar in terms of some key habitat attributes favouring slugs, such as volumetric soil moisture content (mean ± SD: logged, 0.22 ± 0.08 $m^3.m^{-3}$; control, 0.27 ± 0.13 $m^3.m^{-3}$), volume of downed coarse woody debris (64 ± 41 $m^3.ha^{-1}$ and 87 ± 65 $m^3.ha^{-1}$, respectively), and canopy cover (96 ± 3% and 92 ± 4%, respectively) (unpublished data). Low-intensity logging is thus unlikely to have altered the habitat attributes in such a way to make them less suitable for *Arion* (i.e., abiotic resistance), at least 10 to 15 years after logging. Instead, the low-intensity logging event on this site may not have removed biotic resistance to invasion, which can arise from any effect that resident species exerts on invaders, including predation, competition or disease, and may operate alone or in concert with habitat attributes (abiotic and vegetation components) to determine the invasion success of alien species (Levine *et al.*, 2004 ; Ning *et al.*, 2019 ; Pimm, 1989). Competition from resident plant species and herbivory by resident animals commonly regulate plant invasion success (Levine *et al.*, 2004 ; Ning *et al.*, 2019) while interspecific competition and predation from native animals have been shown to slow or prevent the invasion of alien animals (DeRivera *et al.*, 2005 ; Menke *et al.*, 2007). At the Gagnon site, the low-intensity logging event may have favoured the resident species (competitors or predators), resulting in an unsuccessful invasion of *Arion* into logged stands. This potential explanation, however, would need to be tested.

Our study thus suggests that both low- and high-intensity logging events may be detrimental to the invasion success of *Arion*. This finding, when combined with evidence from other studies, suggests that natural (Diez *et al.*, 2012), as well as anthropogenic habitat disturbances (Ning *et al.*, 2019), may create an “invasion window” for alien species (Johnstone, 1986) outside which biological invasions fail. The location of such a window would depend upon the disturbance intensity, and whether or not it relaxes both biotic and abiotic resistance to invasion. Indeed, to favour biological invasion, a disturbance should maintain or make the abiotic conditions suitable for the alien species (i.e., relaxed abiotic resistance), while decreasing the fitness of resident species that compete, prey upon or cause disease to alien species (i.e., relaxed biotic resistance) (Ning *et al.*, 2019). Furthermore, the time that is required for the alien species to benefit from this invasion window may depend upon the stage of the invasion process. Indeed, an alien species at a late stage of the invasion process (e.g., which spreads into locations away from its region of introduction; Blackburn *et al.*, 2011) may more quickly benefit from the invasion window than an alien species that is still establishing (i.e., creating a viable population in the region of introduction). In the latter case, any change in invasion success may go unnoticed for a while because too few individuals were present before the disturbance. In the northeastern Quebec site, *Arion* was poorly established in control stands since it was not detected in 41% of them (Table S1.1), which suggests that *Arion* is at an early stage of the invasion process in this area. This response might explain why it took so much time for *Arion* to become more abundant in logged than in control stands at that site.

Time-since-logging, like logging intensity, is crucial in understanding the effect of logging on the invasion success of alien species. Indeed, *Arion* abundance increased in the years following logging at the north-central Ontario and the northeastern Quebec sites (Table 1.1b). As expected, this increase of *Arion* invasion success over time was higher in the less intense biomass removal plots than in the most intense one (north-central Ontario site). Taken together, these results support the idea that habitat attributes that are suitable for *Arion* may recover over time (e.g., such as the canopy cover at the northeastern Quebec site; Le Borgne *et al.*, 2018a), and that this recovery would take less time with decreasing logging intensity. The recovery of suitable habitat attributes may ultimately promote the invasion success of alien species, as observed at the northeastern Quebec site. However, *Arion* abundance was similar in two-year-old and 10- to 15-year-old logged stands at Kenauk site, which is the only location where logging tended to increase *Arion* abundance. Strayer *et al.* (1986) suggested that gastropod communities (including slugs) might quickly recover from forest disturbance if the vegetation rapidly recovers following a disturbance. If so, then the similar *Arion* abundances in our two-year-old and 10- to 15-year-old logged stands at Kenauk site may be explained by a quick recovery of key habitat attributes for *Arion* after logging. This is supported by the absence of differences among controls, two-year-old, and 10- to 15-year-old logged stands in terms of the volume of coarse woody debris (mean ± SD: control, 72 ± 51 $m^3.ha^{-1}$; two-year-old, 34 ± 26 $m^3.ha^{-1}$; 10- to 15-year-old, 47 ± 60 $m^3.ha^{-1}$) and soil moisture content (mean ± SD: controls, 0.26 ± 0.09 $m^3.m^{-3}$; two-year-old, 0.31 ± 0.09 $m^3.m^{-3}$; 10- to 15-year-old, 0.25 ± 0.01 $m^3.m^{-3}$) (unpublished data).

In light of our results, we propose a more specific formulation of the disturbance hypothesis, as a conceptual framework, based upon the degree to which biotic and abiotic conditions are altered by a disturbance, according to its intensity and time since its occurrence (Figure 1.4). Below an intensity-level threshold, a disturbance could not modify the biotic and abiotic conditions of the ecosystem in a manner that relaxes the biotic and abiotic resistance to the invasion success of alien species. Therefore, biotic and abiotic conditions will still be unsuitable for the alien species despite habitat disturbance, thereby preventing successful invasion. In this scenario, the invasion success of alien species would remain similar (curve 1, Figure 1.4a) or decrease following a disturbance (curve 2, Figure 1.4a), depending upon the way in which biotic and abiotic conditions regulate the alien species abundance. If the disturbance intensity-level is sufficiently high to relax biotic and abiotic resistances within the ecosystem, thereby making it more suitable for the alien species (threshold 1 is overcome, Figure 1.4b), its invasion success would increase following disturbance (Figure 1.4b). This positive disturbance effect may occur more (curve 3, Figure 1.4b) or less quickly following its occurrence (curve 4, Figure 1.4b). Indeed, if the disturbance occurred at the beginning of the invasion process, the alien species may take time to establish, reach reproductive maturity, and increase its abundance in the disturbed sites (Crooks, 2005). Once it is well established, the alien species may reach high densities in the disturbed habitats, even spilling over into adjacent undisturbed habitats (Didham *et al.*, 2007). Finally, if the disturbance is so intense that the abiotic conditions become unsuitable for the alien species (i.e., threshold 2: physiological limits of the species is achieved), invasion success of the alien would either decrease or remain similar over the short-term (Figure 1.4c), depending upon when the disturbance occurred during the invasion process. If the disturbance occurs at the beginning of the invasion process, the decrease in invasion success may remain unnoticed because too few individuals were present to be detected prior to the disturbance. Over time, the invasion success of alien species could be higher (curve 5, Figure 1.4c), similar (curve 6, Figure 1.4c) or lower (curve 7, Figure 1.4c) in the disturbed habitats compared to pre-disturbance conditions, as has been observed in the temporal patterns of native species abundance after a disturbance (e.g., Vance et Nol, 2003). The form of the response will depend upon how the biotic and abiotic conditions evolve following disturbance.

Considering the substantial variation of invasion success that can result in response to habitat disturbance, the proposed conceptual framework, although necessarily broad, was needed. This framework can be applied to alien animals and plants in relation to different types of natural and anthropogenic disturbances (e.g., fire, drought, and logging, among others). It provides a better understanding of the conditions under which habitat disturbance promotes the invasion success of alien species. Even though the effect of habitat disturbance on invasion success of alien species may vary with disturbance type and local environmental conditions (Andersen, 2019 ; Hobbs and Huenneke, 1992 ; Jauni *et al.*, 2015), this framework provides an explicit context within which predictions can be tested regarding the effect of disturbance and its characteristics on the invasion success of alien species. The lack of knowledge on the habitat attributes and interspecific interactions that regulate *Arion* abundance in our forest ecosystems prevents us from explicitly testing this conceptual framework. Testing it on a species with well-known habitat requirements and interspecific relationships would be the next step in acquiring a better understanding of the effect of habitat disturbance on the invasion success of alien species.

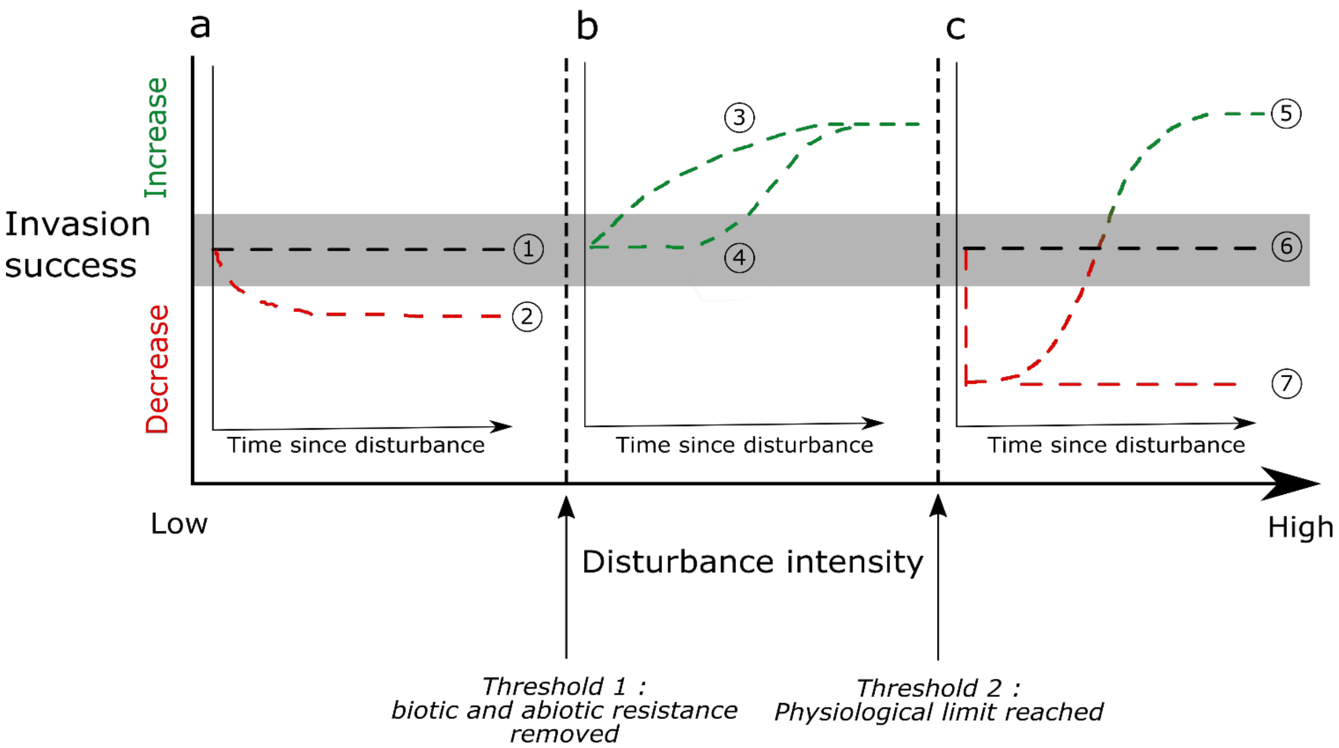


Figure 1.4: Conceptual framework to determine the effects of a disturbance, its intensity, and the time since its occurrence on the invasion success of alien species (e.g., its abundance). See text for a detailed explanation. Values in the shaded area are not distinguishable from pre-disturbance values

1.7 Acknowledgements

We thank Audrey Sigouin, Émilie Roy, Hélène Le Borgne, Andréanne Beardsell, Maxime Cotnoir, Pascal Royer-Boutin, Orphé Bichet, Gabriel Emond, Jean-Pierre Michaud, Laura Boisvert-Marsh, Kerrie Wainio-Keizer, Kevin Good, Craig Zimmerman and Idaline Laigle for their help at different stages of the study. Finally, we also thank WFJ Parsons for English revision.

1.8 Supplementary material

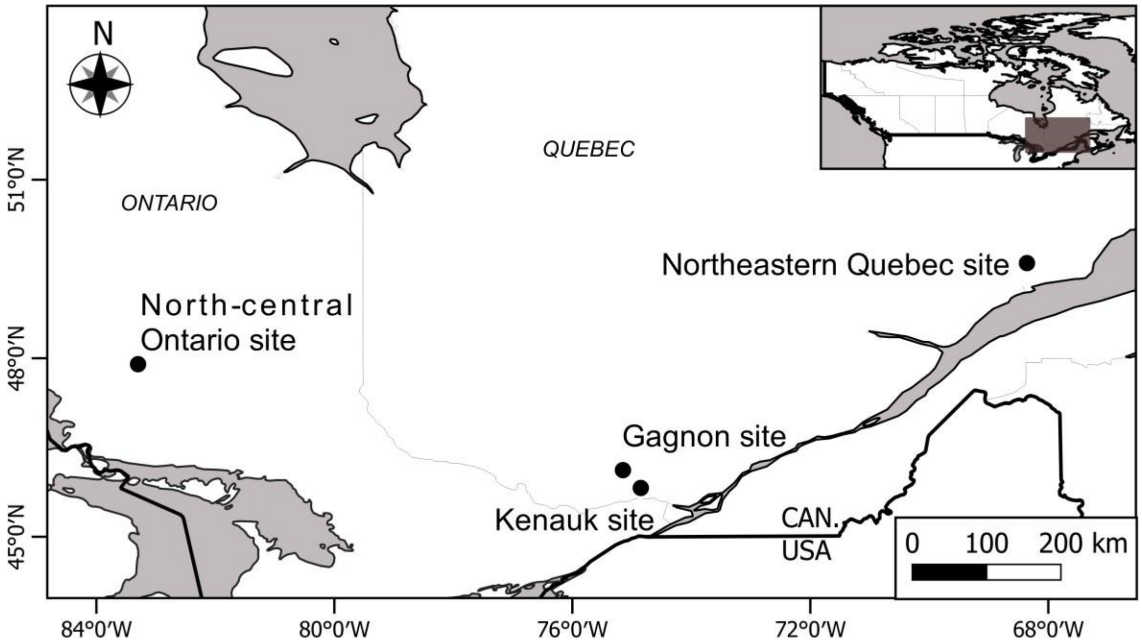


Figure S1.1: Locations of the four study sites. North-central Ontario and northeastern Quebec sites are located in the boreal forest, whereas the Gagnon and Kenauk sites are in the temperate forest

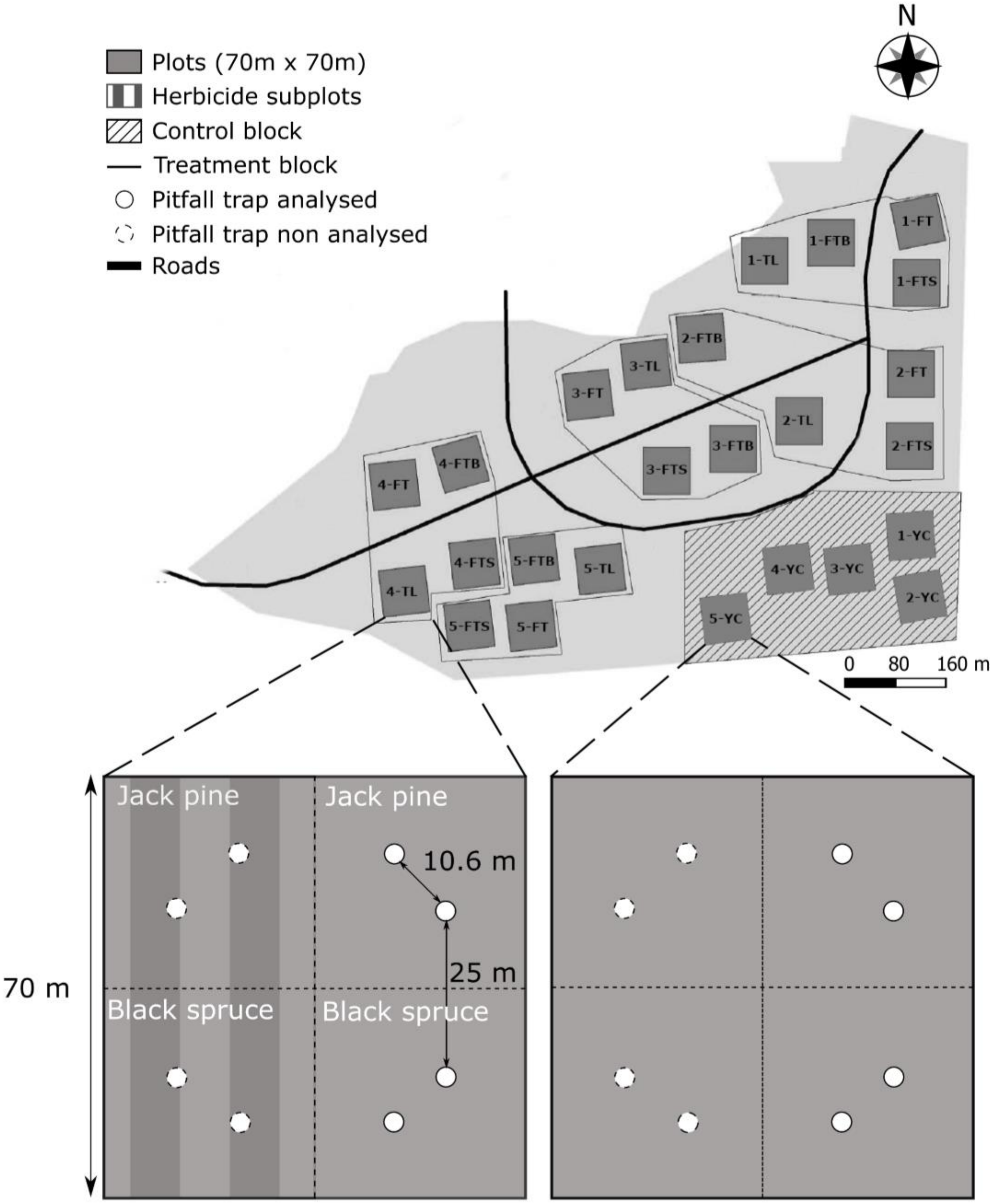


Figure S1.2: Layout of the Island Lake Biomass Experiment in north-central Ontario. Treatments are labelled by block number and biomass removal treatment (TL: tree-length; FT: full-tree biomass; FTS: stumped; FTB: bladed; YC: young control). Figure modified from Venier *et al.* (2017). For further details, see Kwiaton *et al.* (2014)

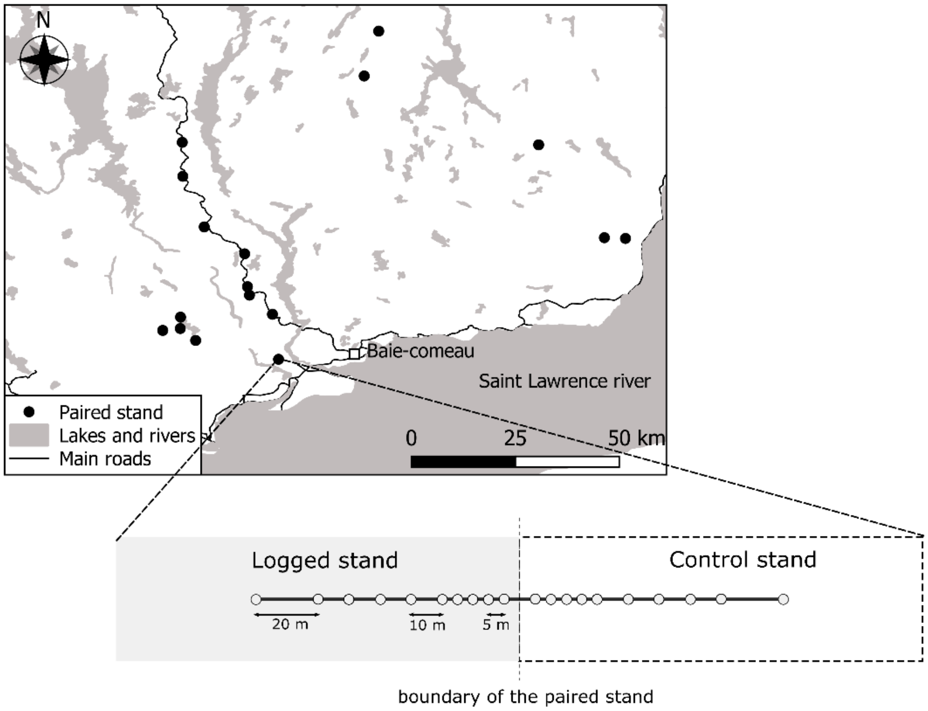


Figure S1.3: Locations of paired stands and pitfall traps layout at the northeastern Quebec site. Ten pitfall traps extended 85 m into each portion of the paired stands, as shown in the inset. Logged and control stands were at least 200 × 250 m and shared a boundary that was ≥ 250 m in length. Figure modified from Dupuch and Fortin (2013)

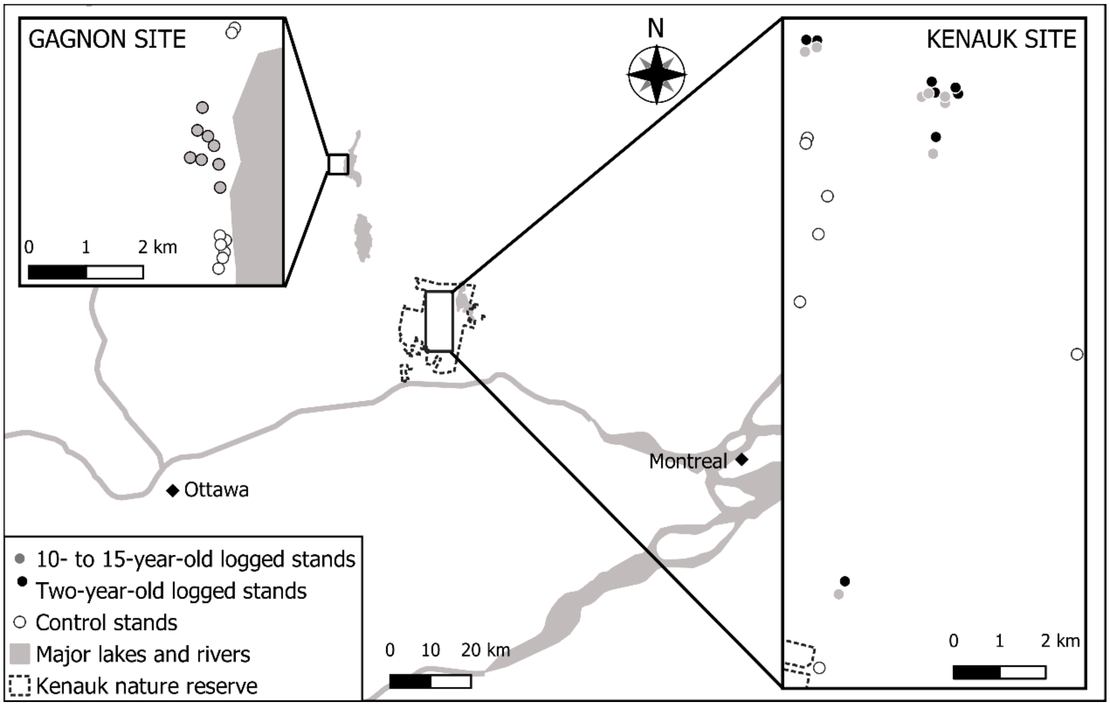
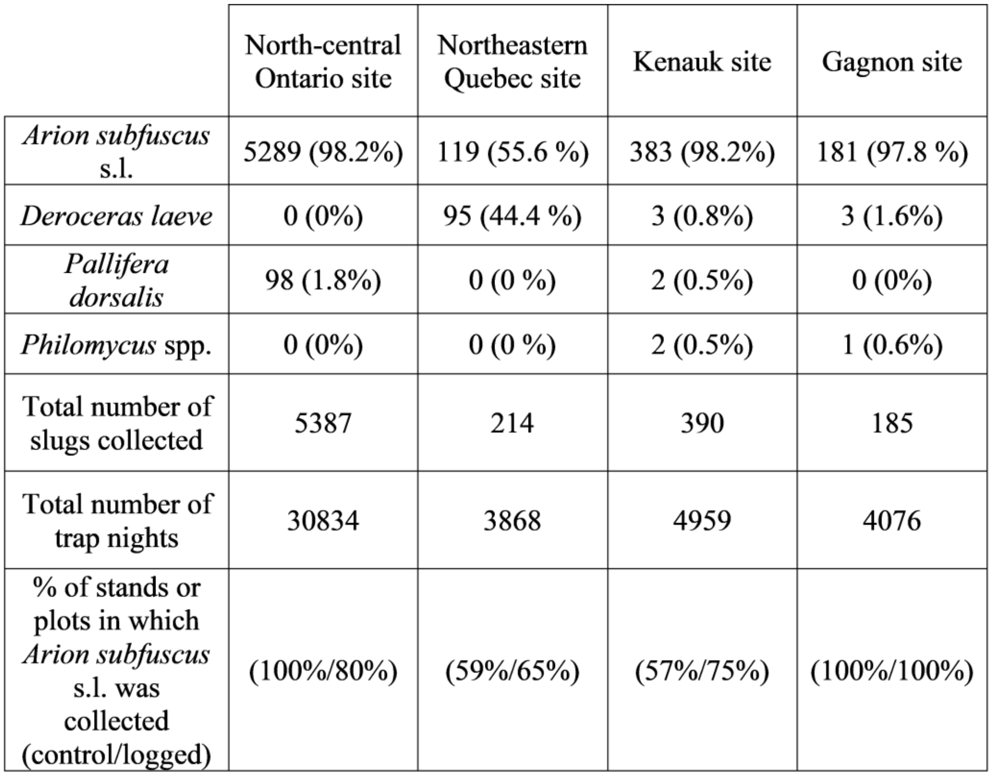


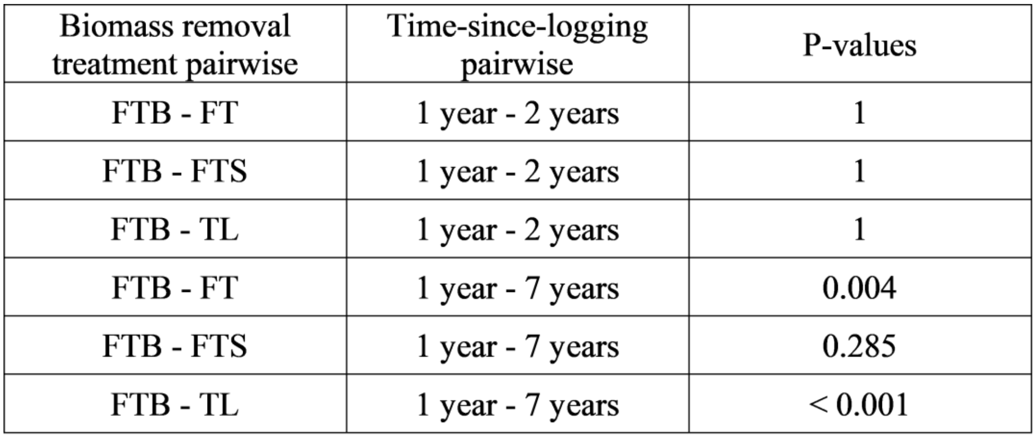
Figure S1.4: Locations of Kenauk and Gagnon sites in southern Quebec. The distribution of the 10- to 15-year-old (grey circle) and two-year-old (black circle) logged stands and control stands (white circle) are shown in insets for each site

Table S1.1: Number of slugs collected at the four study sites. Values in parentheses represent the relative occurrences of individuals for a species (or a genus) within the site



	North-central Ontario site	Northeastern Quebec site	Kenauk site	Gagnon site
Arion subfuscus s.l.	5289 (98.2%)	119 (55.6 %)	383 (98.2%)	181 (97.8 %)
Deroceras laeve	0 (0%)	95 (44.4 %)	3 (0.8%)	3 (1.6%)
Pallifera dorsalis	98 (1.8%)	0 (0 %)	2 (0.5%)	0 (0%)
Philomycus spp.	0 (0%)	0 (0 %)	2 (0.5%)	1 (0.6%)
Total number of slugs collected	5387	214	390	185
Total number of trap nights	30834	3868	4959	4076
% of stands or plots in which *Arion subfuscus* s.l. was collected (control/logged)	(100%/80%)	(59%/65%)	(57%/75%)	(100%/100%)

Table S1.2: Results of the multiple pairwise comparisons following a non parametric analysis of variance on adjusted rank transformed *Arion* abundances corrected for differences in sampling effort (i.e., for each sampling year, abundance per plot divided by the number of trap nights per plot) in the boreal forest of the north-central Ontario site. TL: tree-length; FT: full-tree biomass; FTS: stumped; FTB: bladed. The bladed treatment (i.e., FTB) and the first year following the biomass removal treatment (i.e., 2012) were the reference levels for the categorical variables biomass removal treatment and time-since- logging, respectively. The Holm-Bonferroni corrected P-values are presented



Biomass removal treatment pairwise	Time-since-logging pairwise	P-values
FTB - FT	1 year - 2 years	1
FTB - FTS	1 year - 2 years	1
FTB - TL	1 year - 2 years	1
FTB - FT	1 year - 7 years	0.004
FTB - FTS	1 year - 7 years	0.285
FTB - TL	1 year - 7 years	< 0.001

CHAPITRE II

DO DISTURBANCE-INDUCED HABITAT CHANGES DRIVE ALIEN SPECIES INVASION SUCCESS AND NATIVE SPECIES DECLINE? A CASE STUDY BASED ON SLUG SPECIES INHABITING MANAGED DECIDUOUS FORESTS

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2.1 Résumé

La perturbation de l'habitat peut favoriser le succès d'envahissement des espèces exotiques mais les mécanismes sous-jacents restent peu documentés. Bien que les attributs de l'habitat soient identifiés comme étant des déterminants majeurs des invasions biologiques végétales, leur rôle dans le succès d'envahissement des espèces exotiques dans les habitats perturbés a été peu étudié, en particulier chez les espèces animales. Afin de combler cette lacune, nous avons déterminé si la coupe forestière favorisait i) directement le succès d'envahissement d'un complexe de limaces exotiques, *Arion subfuscus* s.l. (ci-après *Arion*), en rendant les attributs de l'habitat plus favorables pour *Arion*, ou ii) indirectement en favorisant le déclin des limaces indigènes sympatriques du genre *Philomycus* (ci-après *Philomycus*), permettant ainsi à *Arion* de combler le vide laissé par ce déclin. Nous avons estimé la masse corporelle et l'abondance d'*Arion* et *Philomycus* (indicateurs de l'aptitude phénotypique et du succès d'envahissement), ainsi que 10 attributs de l'habitat, dans des peuplements témoins et des peuplements perturbés par des coupes forestières, dans deux sites situés dans la forêt tempérée du sud-est du Canada. Nos résultats suggèrent que, selon le site, les changements de l'habitat générés par la coupe forestière ont favorisé le succès d'envahissement d'*Arion* directement, ou indirectement en causant le déclin de *Philomycus*, permettant à *Arion* de combler le vide résultant de ce déclin. Dans leur ensemble, nos résultats démontrent que les mécanismes favorisant le succès d'envahissement d'*Arion* dépendent de la localisation du site. Cette étude a également souligné l'importance d'évaluer plus d'un indicateur du succès d'envahissement (abondance ou masse corporelle) pour mieux comprendre les mécanismes associés aux invasions biologiques.

Mots clés : invasion biologique, espèce exotique, perturbation de l'habitat, coupe forestière, attributs de l'habitat, limace

2.2 Abstract

Habitat disturbance can promote the invasion success of alien species, but the underlying mechanisms remain unclear. Habitat attributes are known to be major determinants of alien plant invasions. However, their role in promoting alien species invasion success in disturbed habitats has been poorly studied, especially in animal species. To address this gap, we determined if logging can promote the invasion success of an alien slug species complex (*Arion subfuscus* s.l., hereafter *Arion*) i) directly by making the habitat attributes more suitable for it, or ii) indirectly by causing the decline of native sympatric Philomycid slugs (hereafter *Philomycus*), thus allowing *Arion* to fill the void left by native species decline. We surveyed *Arion* and *Philomycus* body- mass and abundance (common measures of fitness and hence of invasion success), together with 10 habitat attributes, in logged and control stands, in two sites located in the temperate forest of southeastern Canada. Our findings suggest that, according to the site, logging directly promoted *Arion* invasion success through logging-induced habitat changes, or indirectly with logging-induced habitat changes leading to *Philomycus* decline and *Arion* filling the void left *Philomycus* decline. Taken together our findings provide evidence that the mechanisms promoting *Arion* invasion success are site-specific. This study also highlighted the importance of assessing more than one proxy of invasion success (abundance or body mass) to better understand the mechanisms associated with successful biological invasions.

Keywords: biological invasion, alien species, habitat disturbance, logging, habitat attributes, slug

2.3 Introduction

In the past decades, interest in biological invasions has led to an explosion of scientific literature trying to understand how alien species become invasive (Alpert *et al.*, 2000 ; Colautti *et al.*, 2004 ; Hayes and Barry, 2008 ; Kolar and Lodge, 2001 ; van Kleunen *et al.*, 2015). These studies have generated several hypotheses (Catford *et al.*, 2009 ; Enders *et al.*, 2020), mainly tested in plant species (Jeschke and Heger, 2018). Among them, the disturbance hypothesis postulates that habitat disturbance promotes the invasion success of alien species (Elton, 1958 ; Hobbs and Huenneke, 1992). Empirical studies provide equivocal support for this hypothesis (Nordheimer and Jeschke, 2018), and rarely aimed to identify the underlying mechanisms promoting successful biological invasions (but see: Chabrerie *et al.*, 2008 ; Huebner, 2021).

According to the disturbance hypothesis, habitat disturbance could modify the environmental conditions to such an extent that the habitat becomes less suitable for native species, adapted to pre-disturbance conditions, leading to a decrease in their abundance (Figure 2.1a). Alien species could then indirectly take advantage of habitat disturbance by ‘filling the void’ left by native species decline (Didham *et al.*, 2005 ; Hobbs and Huenneke, 1992) (hypothesis 1, Figure 2.1a). Although the disturbance hypothesis does not mention this possibility, habitat disturbance could also directly promote successful biological invasions by making the environmental conditions more suitable for alien species (hypothesis 2, Figure 2.1b). It is also possible that habitat disturbance simultaneously makes the environmental conditions less suitable for native species (as stated in hypothesis 1) and more suitable for alien species (as stated in hypothesis 2), thus leading to the formulation of a third hypothesis to explain alien species invasion success (Figure 2.1c). Consistent with the third hypothesis, Parker *et al.* (1993) demonstrated that disturbance (in that case roadbed) simultaneously promoted the invasion success of alien plant species and the decline of native species by increasing potassium, phosphorus, pH, and moisture content since alien and native species densities were respectively positively and negatively correlated to some of these variables. These three hypotheses provide a conceptual framework to identify the mechanisms that favour the invasion success of alien species. However, they have been rarely tested in alien animal species, which makes it difficult to reach accurate conclusions on the role of disturbance-induced habitat changes in successful animal invasions in disturbed habitats.

Forest ecosystems have the highest species diversity for many taxonomic groups (Lindenmayer *et al.*, 2006). However, since the 19th century, they have been increasingly disturbed by commercial harvesting, especially in Canada where it has now replaced natural disturbances as the primary disturbance (Cyr *et al.*, 2009). Among the alien slug species in Canada, the invasive species complex, *Arion subfuscus* (Draparnaud, 1805) sensu lato (Pinceel *et al.*, 2005) has shown a rapid expansion of its distribution in eastern Canada. Although it was only located in few areas in Quebec 50 years ago (Chichester and Getz, 1969), it is now found throughout eastern Canada ecosystems, including mature and logged forests (L'Heureux and Angers, 2018 ; Mazaleyrat *et al.*, *submitted*). Nonetheless, the underlying mechanisms of *A. subfuscus* s.l. successful invasion remain unclear (see also chapter III). Although logging can, depending on its characteristics, favour *A. subfuscus* s.l. invasion success (Mazaleyrat *et al.*, *submitted*), the role of logging-induced habitat changes in its invasion success has not been assessed. Currently, little is known about the distribution and abundance of alien and native slugs in Canada (but see: Grimm *et al.*, 2009). Nonetheless, native slug species that belong to the *Philomycus* genus often co-occur with *A. subfuscus* s.l. in deciduous forest ecosystems of North America (Paustian and Barbosa, 2012). Among them, *P. carolinianus* has been assessed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2019). Although currently unstudied, any impact of logging on this species may have the potential to cause its decline. Logging decreases the canopy cover, and affect several other habitat attributes, such as the volume of coarse woody debris (Angers *et al.*, 2005 ; Pedlar *et al.*, 2002), the tree species composition and understory vegetation (Angers *et al.*, 2005 ; Brassard and Chen, 2006 ; Clark and Covey, 2012 ; Duguid and Ashton, 2013 ; von Oheimb and Härdtle, 2009). Changes in these habitat attributes are known to affect the abundance of many gastropod species in forest ecosystems (Abele *et al.*, 2014 ; Beyer and Saari, 1977, 1978 ; Johnston *et al.*, 2018 ; Kappes, 2005, 2006 ; Müller *et al.*, 2005 ; O'Hanlon *et al.*, 2020). Until now, studies on *A. subfuscus* s.l. or *Philomycus* spp. did not identify key forest habitat attributes that may affect their abundance, which makes it difficult to determine whether logging will make the habitat attributes more or less suitable for each of them.

Thus, our objectives were to determine 1- how logging-induced habitat changes promote *A. subfuscus* s.l. invasion success (i.e., hypotheses 1, 2 or 3; Table 2.1a; objective 1), and 2- if logging promotes *Philomycus* decline, and if so, if it is promoted by logging-induced habitat changes, which is expected with hypotheses 1 and 3 (objective 2). Regardless of the hypothesis that may explain *Arion* invasion success, we expected its abundance and body mass (i.e., common proxies of fitness and invasion success; Jeschke and Heger, 2018) to be higher in logged than in unlogged forests (prediction 1, Table 2.1a). The first hypothesis will be supported if *Arion* abundance or body mass is not related to logging-induced habitat changes (prediction 4, Table 2.1a), whereas *Philomycus* abundance or body mass should be lower in logged than in unlogged forests (prediction 2, Table 2.1a) and decreases with logging-induced habitat changes (prediction 5, Table 2.1a). Alternatively, the second hypothesis would be supported if *Philomycus* abundance and body mass are not affected by logging (prediction 3, Table 2.1a), whereas logging-induced habitat changes should increase *Arion* abundance or body mass (prediction 6, Table 2.1a). The third hypothesis would be supported if logging-induced habitat changes are detrimental to native species (prediction 5, Table 2.1a) and promote alien species invasion success (prediction 6, Table 2.1a).

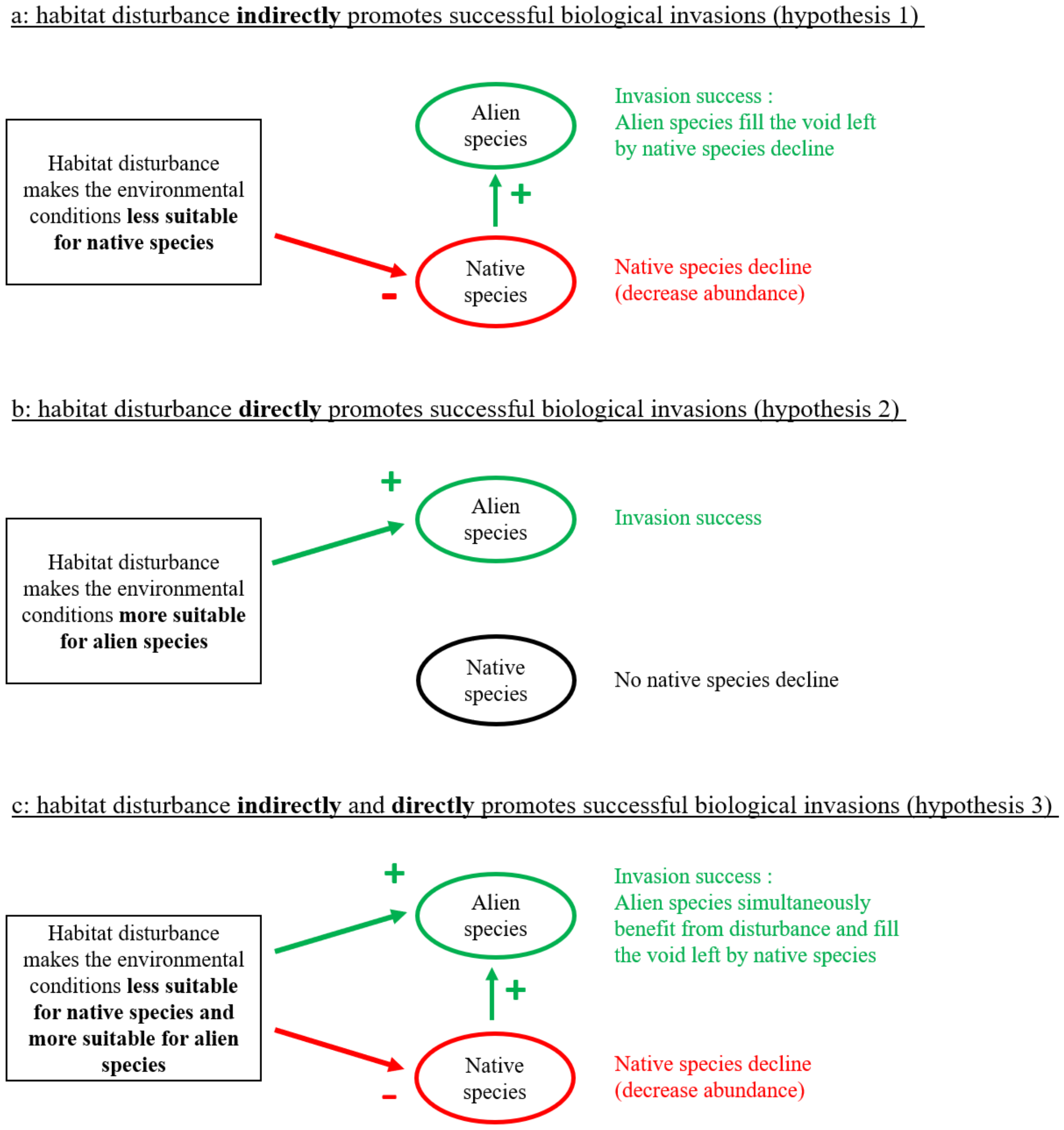


Figure 2.1: Hypotheses showing the mechanisms promoting the invasion success of alien species in disturbed habitats. Green indicates a beneficial effect on alien species invasion success, whereas red indicates a detrimental effect on the abundance of native species

Table 2.1: a. Mechanisms and their predictions that explain successful biological invasions in disturbed habitats. b. Effects of logging and logging-induced habitat changes on species abundance and body mass at our two study sites. See Results section 2.5 for more details on the prediction support. We did not evaluate the effect of logging-induced habitat changes on *Philomycus* if logging did not affect its abundance or body mass

a.

	Species	Abundance/body mass in logged forests compared to unlogged forests	Effect of logging-induced habitat changes on species abundance/body mass
Hypothesis 1: logging **indirectly** promotes the invasion success of alien species	*Arion*	Prediction 1: higher	Prediction 4: no effect
	Philomycus	Prediction 2: lower	Prediction 5: negative
Hypothesis 2: logging **directly** promotes the invasion success of alien species	*Arion*	Prediction 1: higher	Prediction 6: positive
	Philomycus	Prediction 3: similar	Not applicable
Hypothesis 3: logging **indirectly and directly** promotes the invasion success of alien species	*Arion*	Prediction 1: higher	Prediction 6: positive
	Philomycus	Prediction 2: lower	Prediction 5: negative

b.

Site	Species	Abundance/body mass in logged forests compared to unlogged forests	Effect of logging-induced habitat changes on species abundance/body mass
Kenauk	*Arion*	higher	no effect
	Philomycus	lower	negative
Gagnon	*Arion*	higher	positive
	Philomycus	similar	Not applicable

2.4 Materials and methods

2.4.1 Study sites

This study took place in southeastern Canada, in the temperate deciduous forest of southern Quebec in two sites located 40 km apart: inside the Kenauk Nature Reserve (45° 42’ N, 74° 53’ W; hereafter Kenauk site), and near the Gagnon Lake (46° 06’ N, 75° 08’ W; hereafter Gagnon site; Figure 2.2). The two sites are similar in terms of dominant tree species with a canopy cover mainly composed of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.) (Nolet *et al.*, 2015). At Kenauk and Gagnon sites, mean annual temperature (1981–2010) is 5.3 °C and 4.5 °C respectively, while mean annual precipitation (1981–2010) is 1204 mm and 1091 mm respectively (Environment Canada, 2020).

2.4.2 Experimental design and slug sampling

At Kenauk site, we sampled two-year-old logged stands (n = 8), 10- to 15-year-old logged stands (n = 8), and control stands (n = 7, > 50-year-old uneven-aged stands without any sign of recent or old logging activities; Figure 2.2). The two-year-old stands originated from shelterwood cutting in 2014–2015, whereas the 10- to 15-year-old stands had been clear-cut between 1999 and 2004. Both treatments removed more than 60% of the basal area. At Gagnon site, we sampled 10- to 15-year-old logged stands (n = 8) harvested by selection cutting (i.e., 30% basal area removal) in 2006, and control stands (n = 8) in old uneven-aged stands without any sign or record of logging activities (Figure 2.2).

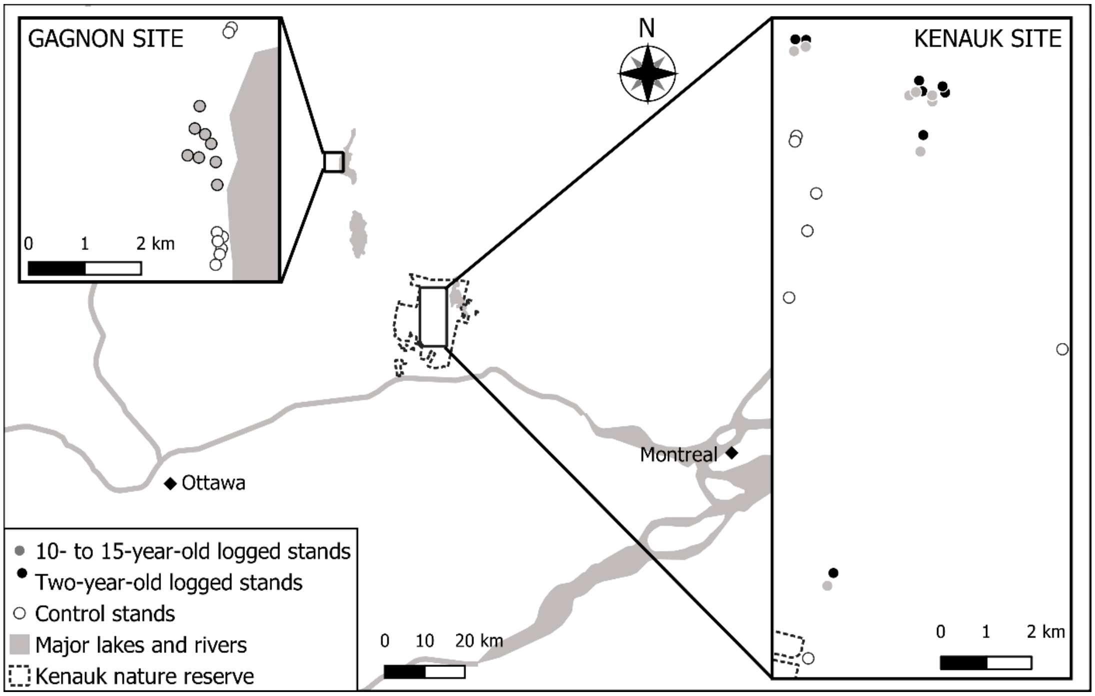


Figure 2.2: Location of Gagnon site and Kenauk site in southern Quebec. The distribution of the 10- to 15-year-old (grey circle) and two-year-old logged stands (black circle), and control stands (white circle) are shown in inset for each site.

Slugs were sampled from June to October 2016 and from May to September 2017. In each stand, we randomly selected a 14 × 14 m plot in which we optimally placed 25 refuge traps (30 × 30 cm sections of 1 cm thick plywood) on the forest floor (i.e., when possible near woody debris or at the base of a tree to maximise our chance to “capture” a slug), a method commonly used to sample slugs (e.g., Hawkins *et al.*, 1997 ; Prezio *et al.*, 1999). Plots were separated from one another by at least 80 m, which should be sufficient to achieve the independence of abundance data among plots. Indeed, a slug species as large as *Philomycus* (i.e., size 7–15 cm, *Arion* is twice smaller) has a home range that covers less than 0.005 ha, which is equivalent to an 8-metre-diameter circle area (Grimm and Paill, 2001). Each time we visited a plot, we counted and identified all slugs on top and beneath each refuge trap. We also carried out a two-observers-five-minutes active search within each plot to compensate for some potential biases linked to species detectability specific to the sampling method. We thus searched for slugs on the dead leaves litter, on the bark of trees or below dead wood, while being careful not to disturb the habitat (e.g., Chichester and Getz, 1969 ; Kappes and Schilthuizen, 2014). This sampling (refuge trapping and active search) was carried when climatic conditions were suitable for slug activity (i.e., 24 hours after a rainfall when the litter surface was moist) to maximise the probability of detecting individuals (Kappes and Schilthuizen, 2014). To avoid potential biases linked to increasing temperature, decreasing soil moisture, and changes in slugs' activity levels as the day progressed, we sampled plots in different orders each sampling day. Every two to four weeks, we weighed individuals found during slug sampling in each plot (OHAUS Scout SPX 123, precision ± 1 mg).

All plots (n = 23 at Kenauk site, n = 16 at Gagnon site) were sampled in 2016, but only a subset of them was sampled in 2017 at Kenauk site (n = 13, three control and ten logged plots) and Gagnon site (n = 15, eight control and seven logged plots) (Table S2.1). Our objective in 2017 was to refine our understanding of the effects of logging on slug body mass and the relationship between *Arion* and *Philomycus* abundances in control plots. We thus sampled plots where both *Arion* and *Philomycus* were present in 2016. Sampled plots were visited at least five times each sampling year (except for two plots at Kenauk site that were visited only three times in 2017). For each sampling year, we estimated *Arion* and *Philomycus* abundances per plot based on the cumulative number of individuals observed with the refuge traps and active search methods combined, and calculated their mean body mass per plot (Table S2.1).

Slugs were identified with external morphological characters (Grimm *et al.*, 2009). *Philomycus* slugs were identified at the genus level since the species cannot be determined with morphological characters only (White-Mclean, 2012). Previous DNA analyses revealed that at least four species were present in our sites: *P. flexuolaris* (Rafinesque, 1820), *P. venustus* (Hubricht, 1953), *P. carolinianus* (Bosc, 1802), and *P. togatus* (Gould, 1841). *Philomycus* genus is an eastern North American genus (White-

Mclean, 2012) but *P. venustus* and *P. carolinianus* have never been reported in Canada (Grimm *et al.*, 2009) and Quebec respectively (COSEWIC, 2019). Dissections of a few *Arion subfuscus* s.l. genitalia (Pinceel *et al.*, 2004) and DNA analysis revealed the presence of *Arion fuscus* in our sites, which is consistent with a previous study suggesting that *A. fuscus* is much more abundant than *Arion subfuscus* s.str. in Quebec (L'Heureux and Angers, 2018). Native *Pallifera dorsalis* (Binney, 1842), and *Deroceras laeve* (Müller, 1774) were also observed but not included in this study since they were rarely encountered.

2.4.3 Characterisation of habitat attributes

At the end of August 2016, we characterised ten habitat attributes in each plot (14 × 14m) (Table S2.2). Within each plot, we identified all tree species (diameter at breast height [DBH]> 9 cm) to assess the tree species richness, and measured their DBH to calculate the basal area ($m^2.ha^{-1}$) of sugar maple and American beech. We also measured the length and diameters at both ends of all coarse woody debris (CWD, diameter at one end> 9 cm, no criteria of length or decomposition) to calculate their volume ($m^3.ha^{-1}$, see: Smalian formula, Köhl *et al.*, 2006). We then summed their volume to compute the total volume of CWD in each plot. We estimated the volume of stumps (diameter> 9 cm, $m^3.ha^{-1}$) by measuring their height and diameter at stump height, and counted the number of snags (DBH> 9 cm, height> 1 m). Furthermore, in each plot, we randomly placed three 2 × 2 m quadrats located 3 m from one another. Within each quadrat, we visually estimated the mean percentage of the ground covered by dead wood (standing dead trees, fallen logs, or branches without any criteria of diameter or length) and dead leaves. We also evaluated the cover of seedlings (<1 cm in diameter and <1 m in height) as the percentage of the ground occupied by the projection of seedling foliage. We then calculated the mean value of dead wood, dead leaves and seedlings cover per plot. Finally, we estimated the canopy closure (%) with a convex densiometer held 1 m above ground level in the centre of each plot.

2.4.4 Statistical analysis

Does logging promote Arion invasion success and Philomycus decline?

To evaluate the effect of logging on *Philomycus* and *Arion* abundances and body mass (predictions 1 to 3, Table 2.1a), we compared their abundance (cumulative number of individuals observed per plot for each sampling year) and mean body mass (log-transformed except for *Arion* at Kenauk site) between plot types in each site. We used generalised linear mixed models (GLMM) with a negative binomial distribution (abundance analyses) or a Gaussian distribution (body mass analyses). At Kenauk site, we initially included the plot type as a three-level-categorical variable (i.e., control, two-year-old logged plots, and 10 to-15-year-old logged plots). However, since these analyses revealed that body mass and abundance of both species did not significantly differ between the two types of logged plots, we used a two-level-categorical fixed variable in subsequent analyses (i.e., logged and control plots as in Gagnon site). For all analyses, we included the plot nested within the sampling year as a random variable, to account for the lack of independence due to repeated observations on the same plot. In abundance analyses, we also added the number of visits (per plot for each sampling year) as an offset variable (log-transformed), to account for differences in unit effort among plots. The offset variable makes model adjustments with its regression coefficient fixed at 1 (Hilbe, 2007).

Does logging affect the habitat attributes?

To determine if logging-induced habitat changes can promote *Arion* invasion success and cause *Philomycus* decline, we first determined if the habitat attributes differed between plot types. To do so, we summarised the variation in the ten habitat attributes (Table S2.2) with a principal component analysis (PCA). Variables were standardised and square root or arcsine transformed when necessary to achieve normality prior to analysis. Then, we determined which habitat attributes gradients best described differences between plot types, by performing two mixed-effect one-way ANOVAs with the first and second principal components (i.e., axes that best-summarised habitat attributes gradients) as dependent variables and the plot type (three-level categorical variable) as an independent variable. P-values were adjusted with a Holm Bonferroni correction to reduce the type I error because we run two ANOVAs (one for each PCA axis). We included the site (two-level categorical variable: Kenauk and Gagnon) as a random variable to account for the lack of independence between plots of the same site. When ANOVAs detected significant differences between plot types, we run posthoc multiple comparisons and adjusted the P-values with a Holm Bonferroni correction to determine which plot types significantly differed from one another (three comparisons).

Does logging-induced habitat changes affect Arion and Philomycus abundance and body mass?

When logging affected *Arion* or *Philomycus* (see the Results section 2.5), we determined if species abundance or body mass were influenced by logging-induced habitat changes (i.e., predictions 4 to 6, Table 2.1a). To do so, we included the scores of the principal components (PCs) that differ between plot types as fixed variables. We used the same model distribution and random variable as those used to evaluate the effect of logging on species abundance and body mass (except for *Arion* body mass at Gagnon that has not been log-transformed prior analysis). For *Philomycus* models, we added *Arion* abundance as a fixed variable (i.e., mean number of individuals observed per visit in each plot for each sampling year) to control for a potential negative effect of *Arion* abundance on *Philomycus* abundance or body mass through competition. We used Akaike's information criterion corrected for small sample size (AICc, Burnham and Anderson, 2002) to rank candidate models that included different combinations of PCs (and *Arion* abundance for *Philomycus* models). In addition, we calculated the difference between the AICc of each model and the lowest AICc observed of all models (i.e., ΔAICc). Models with ΔAICc <2 were equally plausible as the best model to explain the observed patterns in the data (Burnham and Anderson, 2002). If several models had a ΔAICc <2, the most parsimonious model was selected (i.e., with fewer fixed variables). When several models were equally parsimonious, we used conditional model averaging on all the models with ΔAICc <2 to produce the averaged parameter estimates (Burnham and Anderson, 2002).

All analyses were carried out in R v 3.6.3 (R Core Team, 2020) with the package *nlme* for mixed effect ANOVA (Pinheiro *et al.*, 2020), *glmmTMB* for generalised linear mixed models (Brooks *et al.*, 2017), *vegan* for PCA analysis (Oksanen *et al.*, 2019), and *emmeans* for multiple comparisons (Lenth, 2020). Spatial autocorrelation in the data has been checked and none was detected.

2.5 Results

2.5.1 Does logging promote *Arion* invasion success and *Philomycus* decline?

In accordance with prediction 1 (Table 2.1a), logging favoured the invasion success of *Arion* in both sites. Indeed, *Arion* was more abundant (β ± SE: 1.55 ± 0.55, P = 0.005, Figure 2.3a) and had a higher body mass (β ± SE: 0.12 ± 0.04, P = 0.003; Figure 2.3d) in logged than in control plots at Kenauk and Gagnon site respectively. However, *Arion* abundance at Gagnon site (β ± SE: -0.07 ± 0.15, P = 0.643, Figure 2.3b) and its body mass at Kenauk site (β ± SE: -0.05 ± 0.14, P = 0.723, Figure 2.3c) were similar between plot types. *Arion* invasion success co-occurred with *Philomycus* decline only at Kenauk site. Indeed, and in line with the prediction 2 (Table 2.1a), *Philomycus* was less abundant in logged than in control plots at that site (β ± SE: -1.10 ± 0.23, P <0.001, Figure 2.4a), whereas its body mass at that site was similar between plot types (β ± SE: -0.20 ± 0.24, P = 0.406, Figure 2.4c). At Gagnon site, *Philomycus* abundance (β ± SE: 0.34 ± 0.22, P = 0.124, Figure 2.4b) and body mass (β ± SE: 0.07 ± 0.14, P = 0.602, Figure 2.4d) were similar between plot types (supporting prediction 3, Table 2.1a).

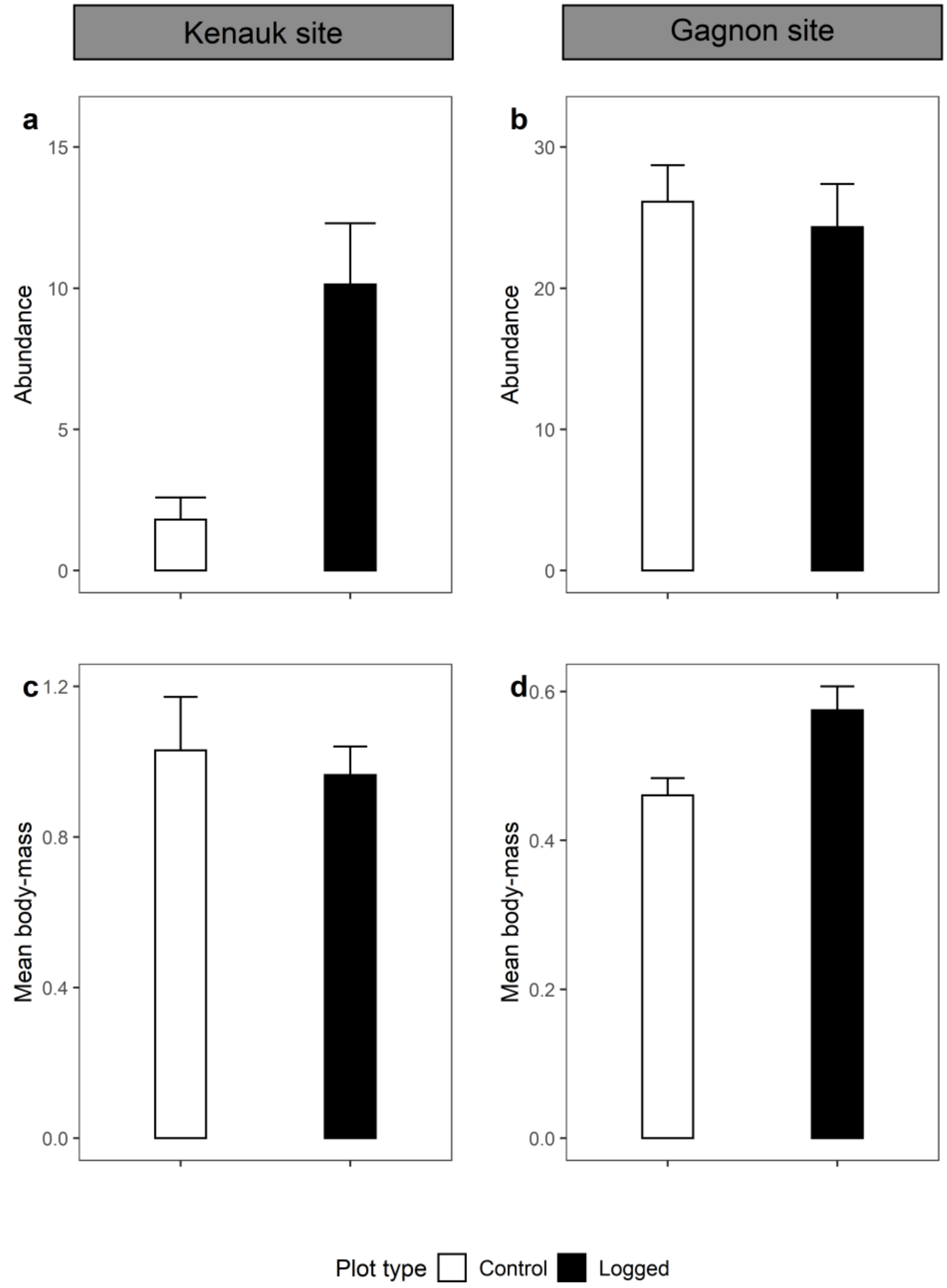


Figure 2.3: *Arion* abundance (mean number.plot^{-1}.visit^{-1}) (a,b) and mean body-mass (g) (c,d) in control (white bar) and logged plots (black bar) at Kenauk site (a,c) and Gagnon site (b,d). Error bars represent standard errors.

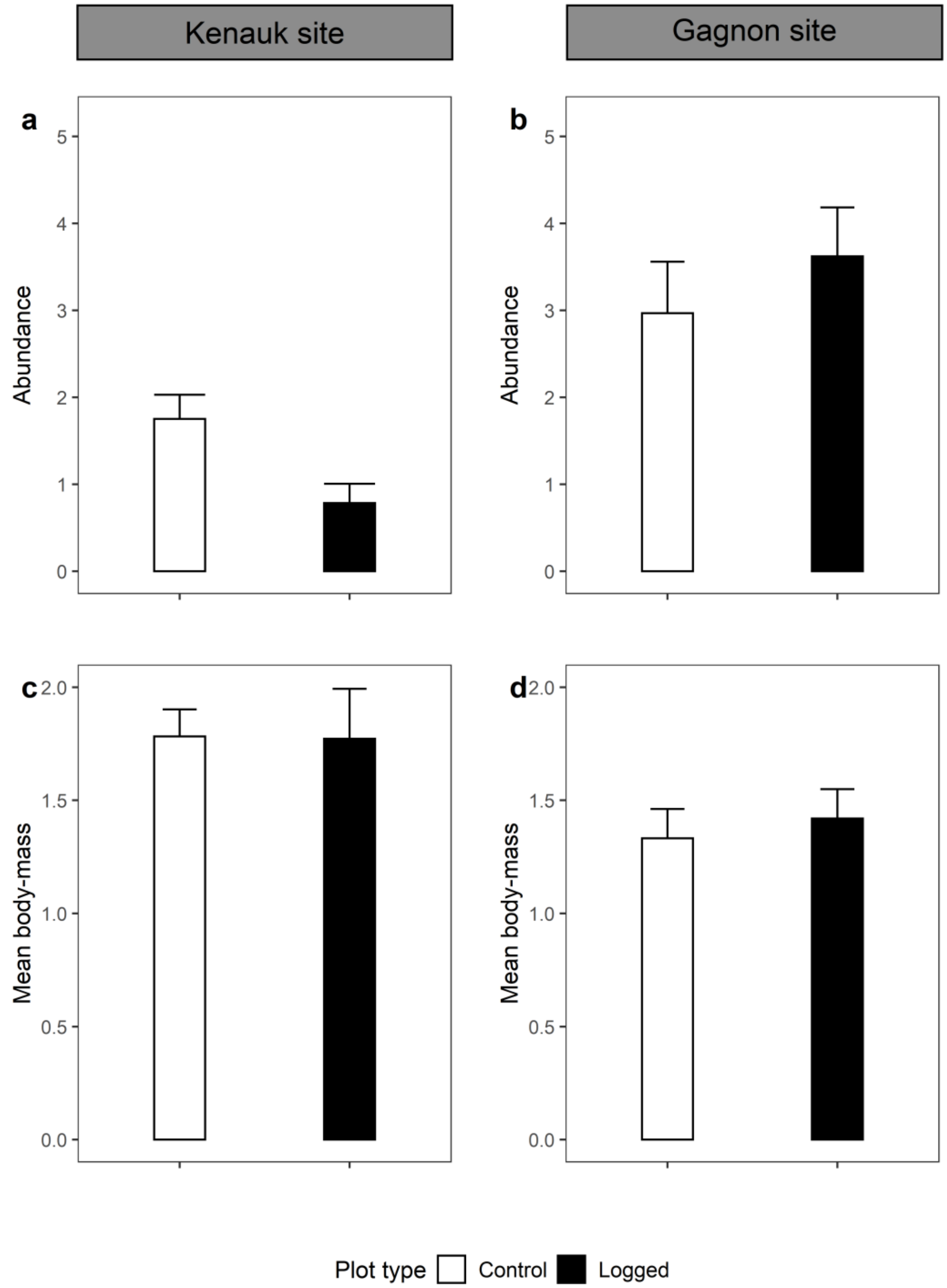


Figure 2.4: *Philomycus* abundance (mean number.plot^{-1}.visit^{-1}) (a,b) and mean body mass (g) (c,d) in control plots (white bar) and logged plots (black bar) at Kenauk site (a,c) and Gagnon site (b,d). Error bars represent standard errors.

2.5.2 Does logging affect the habitat attributes?

Almost half of the variance in the habitat attributes (49%) was explained by the first two principal components (PC1: 27%, PC2: 22%). According to the broken stick criteria, only PC1 was significant while the Kaiser criteria identified the first four PCs as significant. Given that PC3 and PC4 explained individually less than 13% of the variance, they were not considered in the following analyses. PC1 represented a gradient from plots with a high percentage of dead leaves cover and canopy closure to plots with high seedling leaves cover, while PC2 described a gradient from plots with a high basal area of sugar maple and many snags to plots with a high volume of stumps (Figure 2.5). Logging affected the habitat attributes since both PC1 ($F_{2,35} = 20.20$, $P < 0.001$) and PC2 scores differed between plot types ($F_{2,35} = 59.77$, $P < 0.001$). On PC1, two-year-old logged plots had higher scores than 10- to 15-year-old logged plots (β ± SE: 0.47 ± 0.13, P = 0.001) and control plots (β ± SE: 0.56 ± 0.13, P <0.001), but 10- to 15-year-old logged plots had similar scores than control plots (β ± SE: 0.09 ± 0.10, P = 0.385) (Figure 2.5). Similarly, two-year-old logged plots (β ± SE: 0.26 ± 0.09, P = 0.007) and 10-to-15-year-old logged plots (β ± SE: 0.59 ± 0.08, P <0.001) had higher scores on PC2 than control plots, and 10- to 15-year-old logged plots had higher scores than two-year-old logged plots (β ± SE: 0.32 ± 0.09, P = 0.002) (Figure 2.5).

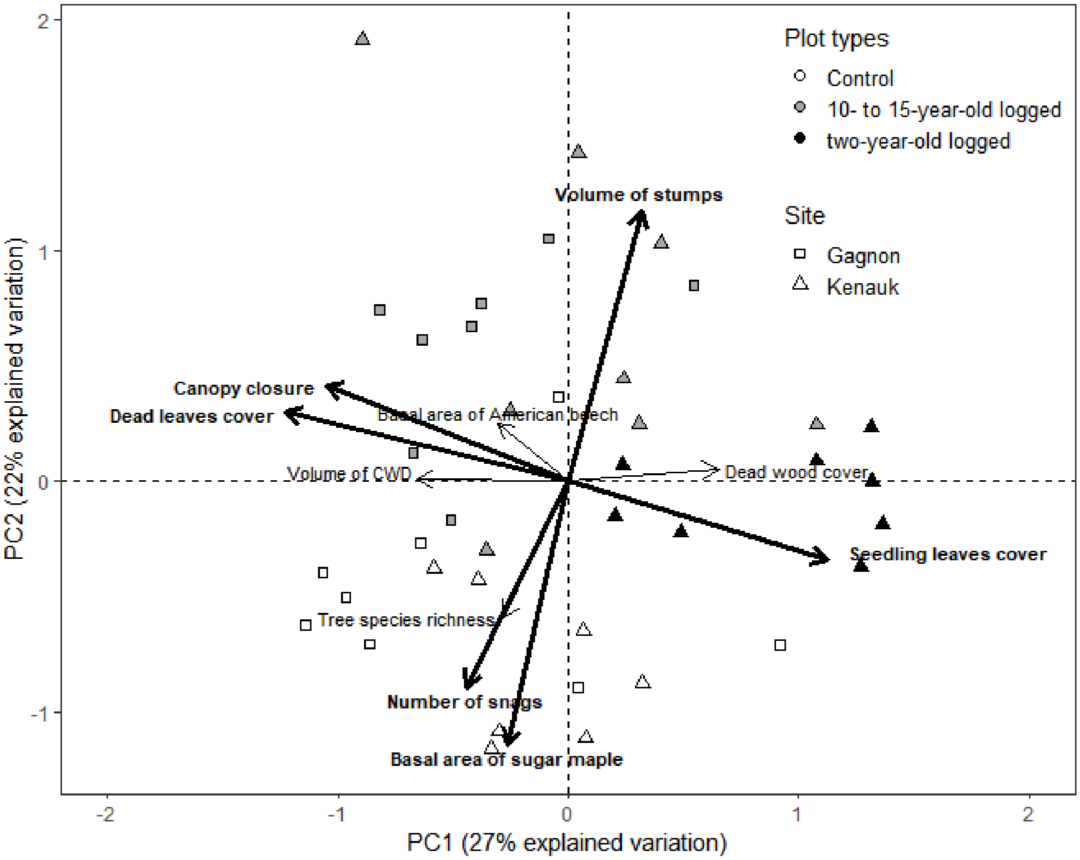


Figure 2.5: First two axes of a principal component analysis (PCA) illustrating variation in ten habitat attributes. Symbols represent plots at Gagnon site (square) and Kenauk site (triangle). Different colours were used to indicate different plot types (white: control plots, grey: 10- to 15-year-old logged plots, and black: two-year-old logged plots). Axes show the proportion of variation in the habitat attributes explained by each principal component. To determine the variables that contribute more than average to PCA space, we computed and drew a circle of equilibrium contribution on the PCA biplot (Borcard *et al.*, 2011, Legendre and Legendre, 2012). Bold arrows and text indicate habitat attributes with a significant contribution on PC1 or PC2.

2.5.3 Does logging-induced habitat changes affect *Arion* and *Philomycus* abundance and body mass?

These logging-induced habitat changes had equivocal effects on *Arion* invasion success. Indeed, model selection indicated that the best model explaining variation in *Arion* mean body mass at Gagnon site included PC2 (Table S2.3). This model showed that the mean body mass of *Arion* increased with PC2 scores (β ± SE: 0.33 ± 0.12, $P < 0.009$, Figure S2.1, which supports prediction 6, Table 2.1a), suggesting that the increase of stump volume and the reduction of sugar maple basal area and snag amount induced by logging has the potential to favour *Arion* invasion success. However, model selection revealed that *Arion* abundance at Kenauk site was neither influenced by PC1 nor PC2 (i.e., the null model was the best model, Table S2.3), which is in accordance with prediction 4 (Table 2.1a). At that site, logging-induced habitat changes had a significant negative effect on *Philomycus* abundance, which supports prediction 5 (Table 2.1a). Indeed, the four best models explaining variation in its abundance included different combinations of PC1 scores, PC2 scores, and *Arion* abundance (Table S2.3) and model-averaging revealed that *Philomycus* abundance decreased with increasing PC1 and PC2 scores (Table S2.4). This finding suggests that the increase of seedling cover and the reduction of dead leaves cover and canopy closure (PC1 gradient), as well as the increase of stump volume and the reduction of sugar maple basal area and number of snags (PC2 gradient) induced by logging can promote *Philomycus* decline.

2.6 Discussion

To our knowledge, this study is the first one to identify how habitat changes induced by a disturbance (i.e., logging) can promote the invasion success of alien animal species and the decline of native species. Our results suggest that *Arion* was more successful in logged than in control plots, but that logging-induced habitat changes were not always directly involved in this successful invasion (Table 2.1b). They also suggest that logging did not always promote *Philomycus* decline, but when it did, it was the result of changes in habitat attributes induced by logging (Table 2.1b).

Our findings reveal that logging promoted *Arion* invasion success and led to decreased *Philomycus* abundance. This is in accordance with previous studies showing that forest management can increase the abundance of alien slug species (*A. subfuscus* s.l. or *A. lusitanicus*: Kappes *et al.*, 2009 ; Mazaleyrat *et al.*, *submitted*) and decrease that of native one (Moore *et al.*, 2002 ; Ovaska *et al.*, 2016). However, these studies did not aim to identify the underlying mechanisms promoting alien slug invasion success in logged forests. We addressed this gap by evaluating if habitat changes induced by logging could directly or indirectly promote *Arion* invasion (Figure 2.1). Previous studies have shown that habitat attributes are key in explaining alien plant invasions (e.g., Quiroz *et al.*, 2011 ; Simonová and Lososová, 2008 ; Truscott *et al.*, 2007), but their role in successful alien animal invasions has been poorly studied (e.g., Kornis *et al.*, 2013 ; Nawrot *et al.*, 2015), especially in a context of anthropogenic disturbance (but see: Chabrerie *et al.*, 2008 ; Lembrechts *et al.*, 2016 ; White *et al.*, 2013 for plants).

As previously observed in temperate forests of North America, tree harvesting at our two sites was associated with a lower tree basal area (Brassard and Chen, 2006) and canopy closure, which are known to increase light availability for plants (Beaudet *et al.*, 2004 ; Perry *et al.*, 2018). This promotes the seedling regeneration and decreased the dead leaves cover in our sites, as observed in other studies (Angers *et al.*, 2005; Perry *et al.*, 2018). Consistent with previous studies, tree harvesting was associated with a reduced amount of snags (Fridman and Walheim, 2000 ; Pedlar *et al.*, 2002), and an increased volume of stumps. These logging-induced habitat changes promoted *Arion* body mass at Gagnon site, but had no effect on *Philomycus* (Table 2.1b) at that site. Until now, no empirical study had investigated the effect of disturbance on the body mass of slugs (but see: Callaham Jr *et al.*, 2003 ; Eggleton *et al.*, 1996 ; Santana

Marques *et al.*, 2020 ; Smith *et al.*, 2008), and our current knowledge of the autecology of slug species in forest ecosystems of North America is very limited (see: Grimm *et al.*, 2009). It is thus difficult to explain the effect of these logging-induced habitat changes on *Arion* invasion success. This finding, however, supports the hypothesis that logging-induced habitat changes directly promotes *Arion* invasion success (hypothesis 2: Figure 2.1b, Table 2.1b).

Similarly to Gagnon site, logging promoted *Arion* invasion success at Kenauk site, but variation in its abundance was not related to logging-induced habitat changes. These changes, however, negatively influenced *Philomycus* abundance at this site. Taken together, these results suggest that *Arion* took advantage of the negative effects of disturbance on *Philomycus* to successfully invade logged forests at Kenauk site, supporting hypothesis 1 (Figure 2.1a, Table 2.1b). Thus, the mechanism promoting *Arion* invasion success seems different between Kenauk and Gagnon sites. Several reasons could explain this discrepancy between our two study sites.

Biological invasions strongly depend on the propagule pressure, the characteristics of the recipient ecosystem (i.e., environmental and biotic conditions), and the characteristics of the invading species (Catford *et al.*, 2009). Successful biological invasions are thus likely to be context-dependent and due to a combination of factors and mechanisms (Catford *et al.*, 2009 ; Williamson and Fitter, 1996), which make the mechanisms promoting alien invasion to vary among sites (D’Antonio, 1993). For example, Taylor *et al.* (2016) demonstrated that the relative importance of propagule pressure, biotic and abiotic factors in promoting the invasion success (i.e., density) of an invasive Pine species (*Pinus contorta*) varied among six ecoregions. This spatial variation in the relative importance of the drivers was due to differences in the plantation age, local vegetation, and climate. Nonetheless, our study is the first one (to our knowledge) to show that mechanisms promoting alien animal invasion can vary among disturbed sites. Our knowledge on the propagule pressure and the characteristics at Kenauk and Gagnon ecosystems is too limited to determine why the mechanisms promoting *Arion* invasion success differ between our study sites. Nonetheless, based on our data, we cannot set aside the idea that competition might be implied. Indeed, our results show a marginally significant negative relationship between *Philomycus* and *Arion* abundances at Kenauk site (Table S2.4). Our data also revealed a negative relationship between the abundance of these species in control plots at Gagnon but not at Kenauk site (Figure S2.2). This suggests that interspecific competition potentially occurs between *Arion* and *Philomycus,* and may contribute along with logging-induced habitat changes, to *Philomycus* decline at Kenauk site. Further studies are needed to determine if these two species really interact through competition and if differences in competition intensity may explain the discrepancy in the mechanisms driving *Arion* invasion success between our sites.

Furthermore, it has been shown that factors influencing species invasion success can be different depending on the proxy used to quantify the invasion success (Stohlgren *et al.*, 1999 ; Truscott *et al.*, 2007). For example, Truscott *et al.* (2007) showed that abiotic factors (e.g., sediment availability) appeared to be the major determinants of occurrence and patch number of the alien riparian plant species *Mimulus guttatus* L., whereas biotic factors (e.g., interspecific competition and grazing) had a greater influence on patch area and stem number per patch of this alien plant species. This is consistent with our findings, which suggest that logging promoted *Arion* abundance at Kenauk site (i.e., indirect effect with *Arion* filling the void left by *Philomycus* decline), but *Arion* body mass at Gagnon site (i.e., direct effect by making the habitat attributes more suitable for *Arion*). These findings highlight the importance of assessing more than one proxy of invasion success to better understand the underlying factors and mechanisms promoting it (Foxcroft *et al.*, 2004 ; Moore and Elmendorf, 2006 ; Rouget and Richardson, 2003 ; Truscott *et al.*, 2007).

2.7 Conclusion

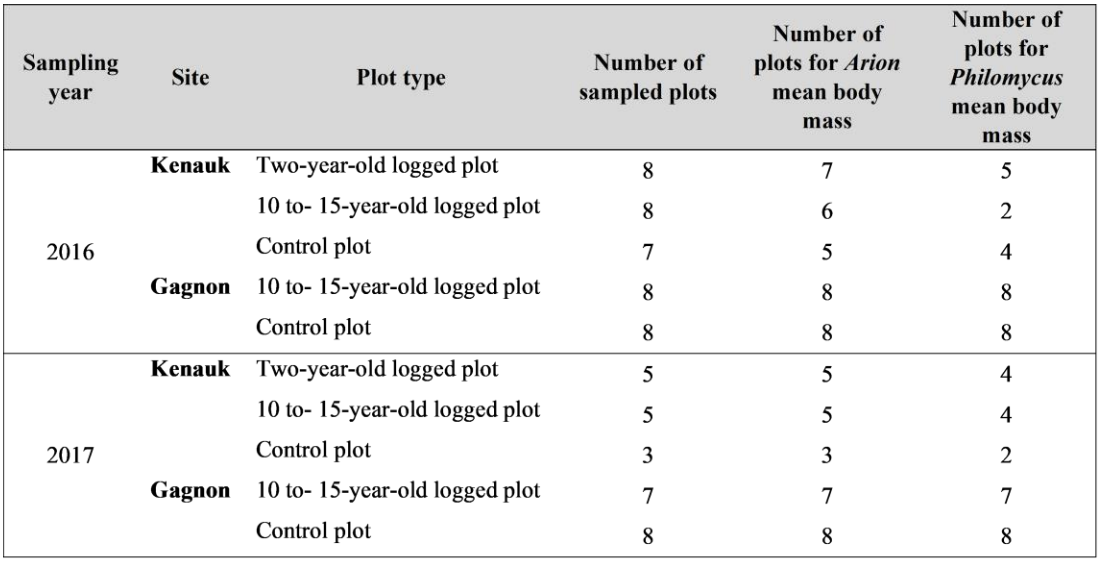
Taken together our findings provide evidence that logging-induced habitat changes can promote directly (hypothesis 2 supported at Gagnon site) or indirectly (hypothesis 1 supported at Kenauk site) *Arion* invasion success. Given that mechanisms promoting invasion success may vary through time and stages of the invasion process (e.g., (Nawrot *et al.*, 2015 ; Theoharides and Dukes, 2007), long-term monitoring of alien and native species in forests could aid to determine if logging-induced habitat changes promote *Arion* invasion success only in a short period of time after logging or at a longer time scale. If alien species invasion success is only the result of disturbance-induced habitat changes, the proxy of invasion success should decrease over time once the disturbance is removed or alleviated (Huebner, 2021 ; Wilson and Pinno, 2013). Given that disturbance is relatively recent (15-year-old logging) in this study, we do not know if logging will promote *Arion* success invasion in the long term (but see: Mazaleyrat *et al.*, *submitted*). Such knowledge is, however, necessary to determine if the role of disturbance-induced habitat changes in alien species invasion success varies through time and if alien species such as *Arion* could become the cause of declines in native species, thus reinforcing their dominance.

2.8 Acknowledgements

The authors kindly thank Émilie Roy et Audrey Mia Sigouin for their assistance in data collection, as well as Émilie Ladent and Samuel Rosner. This research was funded by the Fonds de recherche du Québec – Nature et technologies (FRQNT, grant number 2016-NC-189930) and the Natural Sciences and Engineering Research Council of Canada (NSERC, grant number RGPIN-2015-04516). DNA analyses were funded by the Kenauk Institute.

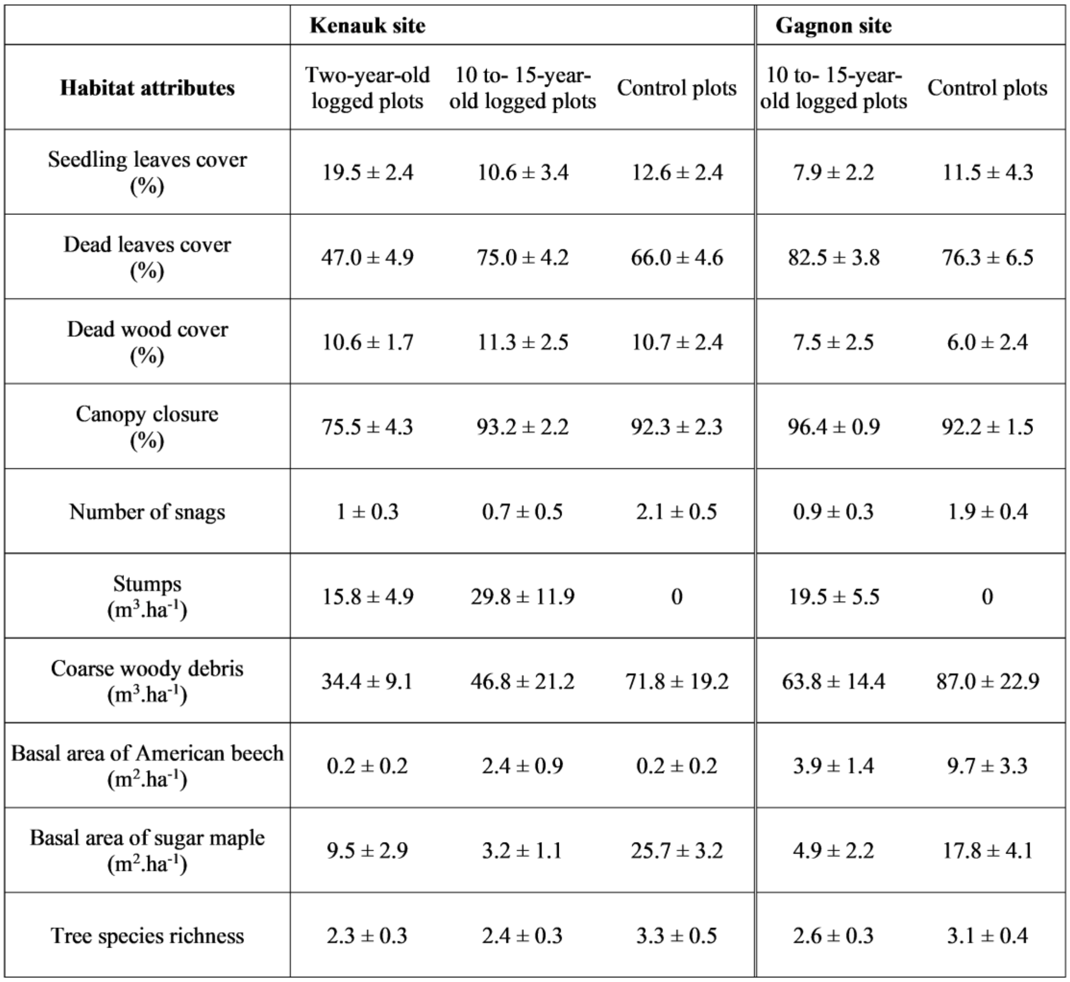
2.9 Supplementary material

Table S2.1: Number of sampled plots in 2016 and 2017 at Kenauk site and Gagnon site, and for which *Arion* and *Philomycus* mean body mass was calculated.



Sampling year	**Site**	**Plot type**	**Number of sampled plots**	**Number of plots for *Arion* mean body mass**	**Number of plots for *Philomycus* mean body mass**
2016	**Kenauk**	Two-year-old logged plot	8	7	5
		10 to- 15-year-old logged plot	8	6	2
		Control plot	7	5	4
	Gagnon	10 to- 15-year-old logged plot	8	8	8
		Control plot	8	8	8
2017	**Kenauk**	Two-year-old logged plot	5	5	4
		10 to- 15-year-old logged plot	5	5	4
		Control plot	3	3	2
	Gagnon	10 to- 15-year-old logged plot	7	7	7
		Control plot	8	8	8

Table S2.2: Mean value of habitat attributes measured in the different plot types at Kenauk and Gagnon site (± standard error).



	Kenauk site			**Gagnon site**	
Habitat attributes	Two-year-old logged plots	10 to- 15-year-old logged plots	Control plots	10 to- 15-year-old logged plots	Control plots
Seedling leaves cover (%)	19.5 ± 2.4	10.6 ± 3.4	12.6 ± 2.4	7.9 ± 2.2	11.5 ± 4.3
Dead leaves cover (%)	47.0 ± 4.9	75.0 ± 4.2	66.0 ± 4.6	82.5 ± 3.8	76.3 ± 6.5
Dead wood cover (%)	10.6 ± 1.7	11.3 ± 2.5	10.7 ± 2.4	7.5 ± 2.5	6.0 ± 2.4
Canopy closure (%)	75.5 ± 4.3	93.2 ± 2.2	92.3 ± 2.3	96.4 ± 0.9	92.2 ± 1.5
Number of snags	1 ± 0.3	0.7 ± 0.5	2.1 ± 0.5	0.9 ± 0.3	1.9 ± 0.4
Stumps ($m^3.ha^{-1}$)	15.8 ± 4.9	29.8 ± 11.9	0	19.5 ± 5.5	0
Coarse woody debris ($m^3.ha^{-1}$)	34.4 ± 9.1	46.8 ± 21.2	71.8 ± 19.2	63.8 ± 14.4	87.0 ± 22.9
Basal area of American beech ($m^2.ha^{-1}$)	0.2 ± 0.2	2.4 ± 0.9	0.2 ± 0.2	3.9 ± 1.4	9.7 ± 3.3
Basal area of sugar maple ($m^2.ha^{-1}$)	9.5 ± 2.9	3.2 ± 1.1	25.7 ± 3.2	4.9 ± 2.2	17.8 ± 4.1
Tree species richness	2.3 ± 0.3	2.4 ± 0.3	3.3 ± 0.5	2.6 ± 0.3	3.1 ± 0.4

Table S2.3: Models predicting *Arion* abundance and body mass at Kenauk and Gagnon site respectively, as well as *Philomycus* abundance at Kenauk site. The Akaike Information Criterion corrected for small sample size (AICc), and the differences in AICc from the lowest scoring model are shown. The effect of PCs scores on *Arion* body mass at Kenauk site, *Arion* abundance at Gagnon site, *Philomycus* body mass and abundance at Gagnon site, and *Philomycus* body mass at Kenauk site were not tested because they did not significantly differ between plot types (see the Results section 2.5). Bold text indicates the selected models. Bold models for *Philomycus* abundance were used to produce estimates based on conditional model-averaging

Species	Site	Dependent variable	Independent variable	AICc	ΔAICc
Arion	Kenauk	Abundance	**Null**	**337.93**	**0.00**
			PC2	340.21	2.27
			PC1	340.54	2.60
			PC1 + PC2	343.08	5.14
	Gagnon	Body mass	**PC2**	**0.00**	**0.00**
			PC1 + PC2	3.10	3.10
			Null	3.31	3.31
			PC1	6.03	6.03
Philomycus	Kenauk	Abundance	**Arion abundance + PC1 + PC2**	**209.31**	**0.00**
			PC1 + PC2	**210.15**	**0.84**
			Arion abundance + PC2	**210.39**	**1.08**
			Arion abundance + PC1	**211.02**	**1.70**
			PC2	211.38	2.06
			PC1	212.31	3.00
			Arion abundance	212.50	3.18
			Null	214.31	5.00

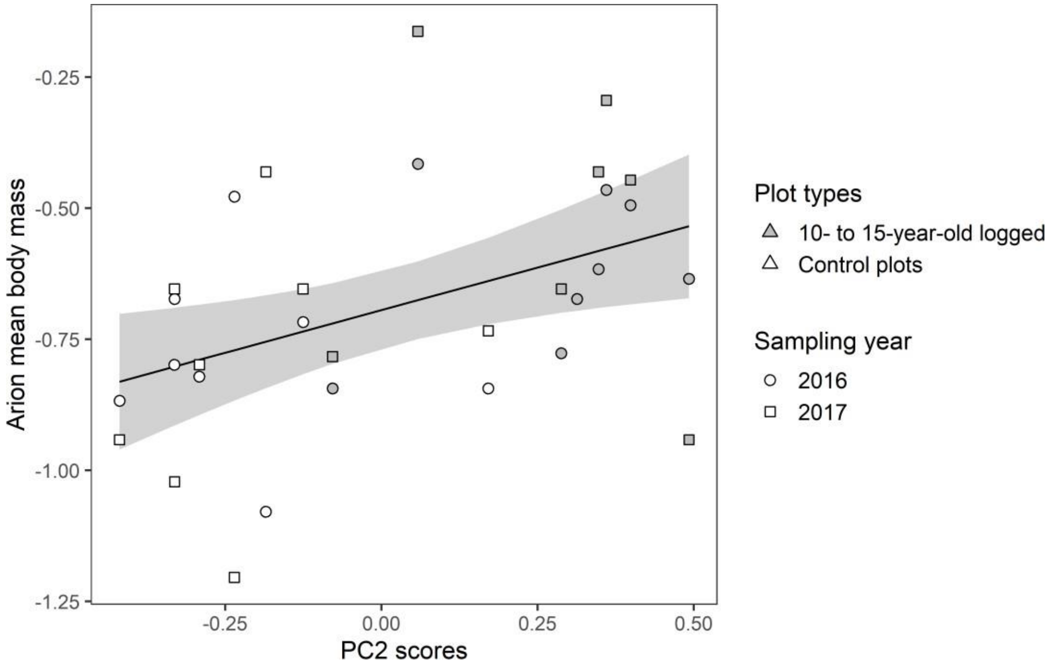


Figure S2.1: *Arion* mean body mass (g, log-transformed) in plots in function of the PC2 scores in control plots (white symbol) and 10- to 15-year-old logged plots (grey symbol). Different shapes were used to indicate different sampling year (2016: circle, 2017: square). Regression line enclosed by shaded confidence interval (95%) is plotted

Table S2.4: Model-averaged estimates, standard errors, Z-values, and P-values for variables included within the four models predicting the abundance of *Philomycus* at Kenauk site (see Table S2.3). Independent variables were scaled before model averaging

	Estimate	Standard error	Z-value	P-value
Intercept	-0.03	0.33	0.07	0.941
PC2	-0.31	0.15	2.01	0.045
PC1	-0.28	0.13	1.98	0.048
Arion abundance	-0.31	0.16	1.90	0.058

To determine if *Arion* may be involved in *Philomycus* decline, we tested if a negative relationship existed between its abundance (mean number of individuals observed per visit in each plot for each sampling year) and that of *Arion* (as a fixed variable) in control plots. We used two linear mixed models (one model for each site) and included the plot nested within the sampling year as a random variable. Given that changes in abiotic conditions might force competition, or conversely relax it (e.g., Alcaraz *et al.* 2008), we also included the sampling year and its interaction with *Arion* abundance as fixed variables. We did not include this interaction at Kenauk site because our dataset was too small in 2017 (n = 3). *Arion* may threaten *Philomycus* population at Gagnon site since its abundance was negatively related to *Arion* abundance in control plots in 2017 (significant interaction *Arion* abundance × sampling period, β ± SE: -0.25 ± 0.09, P = 0.006). Such a relationship was, however, absent in 2016, as well as at Kenauk site (β ± SE: -0.06 ± 0.09, P = 0.497).

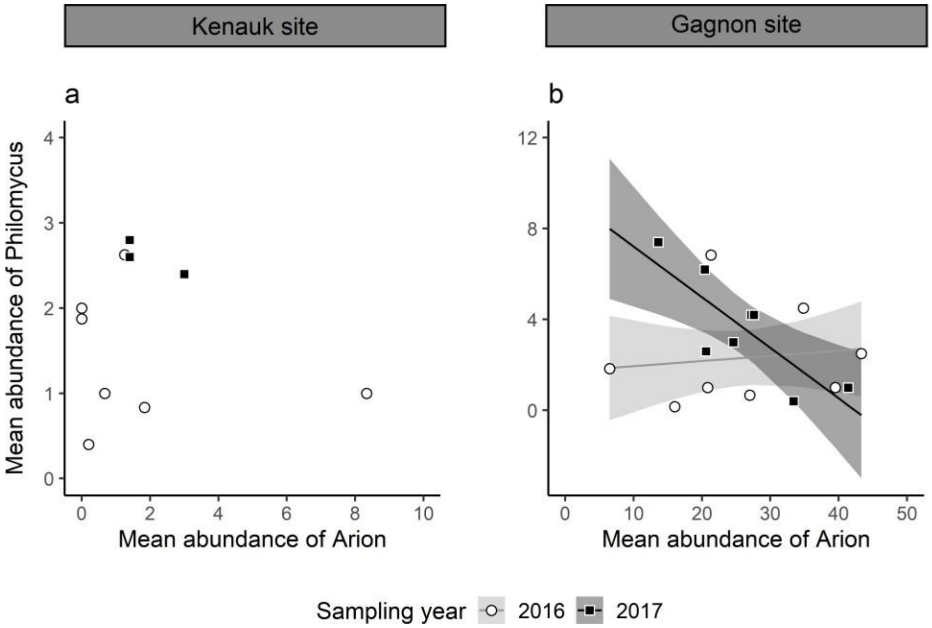


Figure S2.2: Mean abundance of *Philomycus* (plot^{-1}.visit^{-1}) in function of the mean abundance of *Arion* (plot^{-1}.visit^{-1}) in control plots in 2016 (white circle) and 2017 (black square) at Kenauk site (a) and Gagnon site (b). Regression lines enclosed by shaded confidence intervals are plotted for 2016 (grey) and 2017 (black). Shades correspond to the 95% confidence intervals

CHAPITRE III

INVASION SUCCESS OF ALIEN SLUG SPECIES IN DISTURBED HABITATS: TESTING THE ROLE OF BEHAVIOURAL PHENOTYPE AND PLASTICITY, AS WELL AS INTERSPECIFIC COMPETITION UNDER CONTROLLED CONDITIONS

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3.1 Résumé

La perturbation de l'habitat peut favoriser le succès d'envahissement des espèces exotiques mais les mécanismes sous-jacents restent cependant peu documentés, tout particulièrement chez les espèces animales. D'une part, les espèces exotiques pourraient présenter des valeurs de traits qui facilitent l'envahissement (hypothèse de l'envahisseur idéal) ou une plus grande plasticité phénotypique que les espèces indigènes (hypothèse de la plasticité phénotypique), ce qui favoriserait leur succès d'envahissement dans les habitats perturbés. D'autre part, les espèces exotiques pourraient être plus compétitrices que les espèces indigènes. Nous avons effectué des expériences en milieu contrôlé pour déterminer lequel de ces mécanismes pouvait expliquer le succès d'envahissement d'*Arion subfuscus* s.l. (ci-après *Arion*), un complexe de limaces exotiques que l'on retrouve dans plusieurs écosystèmes perturbés de l'est du Canada, telles que les forêts aménagées. Pour cela, nous avons comparé les réponses comportementales d'*Arion* et celles de limaces indigènes sympatriques du genre *Philomycus* (ci-après *Philomycus*) face à une diminution de la teneur en eau du sol, un phénomène généralement observé suite à l'ouverture de la canopée générée par une coupe forestière. Nous avons également déterminé si la présence d'*Arion* affectait le comportement de *Philomycus*, ce qui indiquerait qu'*Arion* a une plus grande capacité compétitrice par interférence que les espèces indigènes. Nos résultats montrent qu'*Arion* n'avait ni un niveau d'audace et d'activité exploratoire (c.-à-d. des comportements qui favorisent le succès d'envahissement), ni une plasticité phénotypique plus élevée que *Philomycus*, et que sa présence n'avait pas affecté le comportement des espèces indigènes. *Arion* pourrait toutefois exploiter plus efficacement les ressources que les espèces indigènes puisqu'elle utilisait principalement le refuge le plus proche de la nourriture. Les résultats soutiennent l'hypothèse de l'envahisseur idéal, mais ne soutiennent pas l'hypothèse de la plasticité phénotypique ni le fait que la compétition par interférence puisse avoir favorisé le succès d'envahissement d'*Arion* dans les habitats perturbés, tels que les forêts aménagées. Les résultats suggèrent également que la direction et non l'amplitude de la plasticité comportementale pourrait être un mécanisme favorisant le succès d'envahissement des espèces exotiques dans les habitats perturbés.

Mots clés : espèce exotique, perturbation de l'habitat, hypothèse de l'envahisseur idéal, hypothèse de la plasticité phénotypique, compétition par interférence, coupe forestière, limace

3.2 Abstract

Habitat disturbance can promote the invasion success of alien species, but the underlying mechanisms remain unclear, especially in animal species. On the one hand, alien species may have traits values that facilitate invasion (ideal weed hypothesis) or greater phenotypic plasticity than native species (phenotypic plasticity hypothesis), thus promoting their invasion success in disturbed habitats. On the other hand, alien species may have a greater competitive ability than native species. We performed experiments in controlled conditions to determine which of these mechanisms could explain the invasion success of *Arion subfuscus* s.l. (hereafter *Arion*), an alien slug species complex that lives in various disturbed ecosystems of eastern Canada such as managed forests. To do so, we compared the behavioural responses of *Arion* and native sympatric Philomycid slugs (hereafter *Philomycus*) to a decrease in soil moisture content, which often occurs after forest harvesting. We also investigated whether the presence of *Arion* alters *Philomycus* behaviour which would indicate that *Arion* has a greater ability to compete by interference than native species. We showed that *Arion* has neither higher boldness and activity-exploratory levels (i.e., behaviours that promote invasion success) nor greater plasticity than *Philomycus*, and that the presence of *Arion* did not affect the behaviour of *Philomycus*. However, *Arion* may more efficiently exploit the resources than native species since it mainly used the closest refuge from the food source. These findings are in line with the ideal weed hypothesis, but do not support the phenotypic plasticity hypothesis or any role of interference competition in *Arion* invasion success in disturbed habitats such as logged stands. This study also suggests that the direction and not the magnitude of behavioural plasticity might be a key aspect in alien species invasion success in disturbed habitats.

Keywords: alien species, habitat disturbance, ideal weed hypothesis, phenotypic plasticity hypothesis, interference competition, logging, slug

3.3 Introduction

Studies on biological invasions have generated numerous explanations of how alien species become invasive (Enders *et al.*, 2020). Among them, the disturbance hypothesis postulates that habitat disturbance promotes the invasion success of alien species (Elton, 1958 ; Hobbs and Huenneke, 1992). This hypothesis has been mainly tested with alien plants and its support is equivocal (Lozon and MacIsaac, 1997 ; Nordheimer and Jeschke, 2018). Moreover, this hypothesis does not clearly identify the underlying mechanisms involved in alien species invasion success in disturbed habitats.

One line of reasoning is that alien species could benefit from habitat disturbance through phenotypic plasticity − i.e., the ability of a genotype to produce distinct phenotypes, including behavioural traits, when exposed to different and potentially novel environments (Schlichting, 1986). The phenotypic plasticity hypothesis suggests that invasive alien species may be more phenotypically plastic than non-invasive or native ones (Baker, 1965 ; Richards *et al.*, 2006), which allows them to maintain their fitness (i.e., survival and reproduction) in unfavourable environments (Jack-of-all-trades scenario), or to increase their fitness in favourable environments (Master-of-some scenario) (Richards *et al.*, 2006). Greater phenotypic plasticity would enable invasive alien species to express more advantageous phenotypes than native species, and thus enhance their establishment and spread into novel environments such as disturbed habitats (Matesanz *et al.*, 2010). This hypothesis has been widely tested for plants species and is rather well supported (Davidson *et al.*, 2011 ; Funk, 2008 ; Torchyk and Jeschke, 2018, but see Godoy *et al.*, 2011 ; Matzek, 2012). However, studies evaluating the plasticity hypothesis in animal species are less common (Torchyk and Jeschke, 2018, but see: Chown *et al.*, 2007 ; Dzialowski *et al.*, 2003 ; Phillips *et al.*, 2020) and are difficult to compare with those carried out on plant species since plastic response in animal species can involve behavioural changes. Several behaviours could promote successful animal invasions (Chapple *et al.*, 2012), but their plasticity in response to environmental changes mediated by anthropogenic activities has rarely been tested. It is thus still unclear if habitat disturbance promotes the invasion success of alien animal species because they have greater behavioural plasticity compared to native species.

Another line of reasoning is that alien species may have trait values that facilitate invasion success (ideal weed hypothesis, Baker, 1965) rather than greater phenotypic plasticity compared to native species (e.g., Godoy *et al.*, 2011). Such studies are, however, uncommon in animal species (but see: Damas-Moreira *et al.*, 2019 ; Phillips *et al.*, 2020). Several studies have shown that invasive alien animal species are more exploratory (Bubb *et al.*, 2006 ; Chapple *et al.*, 2011 ; Damas-Moreira *et al.*, 2019 ; Rehage and Sih, 2004), bolder (Damas-Moreira *et al.*, 2019 ; Monceau *et al.*, 2015) or more aggressive (Rowles and O'Dowd, 2007 ; Usio *et al.*, 2001) than native species. These behaviours could promote the dispersion and establishment in new environments (Monceau *et al.*, 2015 ; Rehage and Sih, 2004), as well as more efficient foraging (Pintor and Sih 2009), which can promote the invasion success of alien species (Chapple *et al.*, 2012).

Finally, interspecific interactions could play a role in the invasion success of alien species in disturbed habitats (Didham *et al.*, 2005). Indeed, habitat disturbance, by promoting the invasion success of alien species (e.g., increase in their abundance through disturbance-mediated habitat changes), could increase the magnitude of their impacts on native species and thus promote the competitive exclusion of native species (Didham *et al.*, 2007). Several studies have shown that competition with native species (through exploitation or interference) may be a mechanism involved in the invasion success of alien animal species (Carpintero and Reyes-López, 2008 ; Duckworth and Badyaev, 2007 ; Human and Gordon, 1996). Higher levels of aggression, as well as of exploration, activity and boldness, may promote the exploitation of resources and ultimately give invasive animal species a competitive advantage over native species

(Damas-Moreira *et al.*, 2019). In particular, aggressive behaviours may allow them to pre-emptively access limited resources (e.g., Usio *et al.*, 2001) or to a greater amount of resources (e.g., Le Louarn *et al.*, 2016). For example, the Argentine ant (*Linepithema humile*) aggressively displace native ants from bait sites, leading to native species decline, and allowing the Argentine ant greater access to food, thus favouring population growth and invasion success (Rowles and O'Dowd, 2007). To lessen the strength of interference competition, subordinate species may exploit shared resources at different times or locations to minimise the temporal or spatial overlap with the dominant species (e.g., Valeix *et al.*, 2007). These behavioural changes may lead subordinate species to exploit poorer quality habitats or suboptimal activity periods (e.g., when predation risk is higher; Söderbäck, 1994), which in turn will decrease their fitness, leading to subordinate population decline or even extinction in presence of the dominant species (Finstad *et al.*, 2011 ; Langeland *et al.*, 1991). Despite the explosion of scientific literature trying to understand how alien species become invasive (Alpert *et al.*, 2000 ; Matzek, 2012 ; Ordonez *et al.*, 2010 ; van Kleunen *et al.*, 2010), empirical studies showing how advantageous trait values, phenotypic plasticity and competition favour the invasion success of alien animal species in disturbed habitats are still uncommon.

To acquire such knowledge, we used slugs as a biological model. Among the alien slug species in Canada, the species complex, *Arion subfuscus* (Draparnaud, 1805) sensu lato has shown a rapid expansion of its distribution in eastern Canada. Indeed, while 50 years ago the species complex was only located in few areas in Quebec (Chichester and Getz, 1969), it is now found throughout eastern Canada ecosystems, including forests (L'Heureux and Angers 2018; Mazaleyrat *et al.*, *submitted*). Nonetheless, the underlying mechanisms of *A. subfuscus* s.l. successful invasion in eastern Canada forest ecosystems are still unclear. Since the 19th century, forest ecosystems in North America have been increasingly disturbed by commercial harvesting (Wynn, 2017). In several regions, harvesting has now replaced natural disturbances such as wildfires and insect outbreaks as the primary disturbance (Cyr *et al.*, 2009). Slugs are very sensitive to soil moisture content or humidity, and too low soil moisture content can decrease their clutch size, as well as the percentage and number of hatched eggs (Kozłowski, 2009 ; Slotsbo *et al.*, 2013 ; Willis *et al.*, 2008). Since the soil moisture content can be decreased following logging (Chen *et al.*, 1993), disturbed forests could be less suitable for hygrophilous species such as slugs (Kappes, 2006 ; Kappes and Schilthuizen, 2014). However, alien slugs could be less sensitive to disturbance than native slugs and habitat disturbance can even favour their invasion success (Mazaleyrat *et al. submitted*; Kappes 2006; Kappes and Schilthuizen 2014). Although land slugs and snails can travel long distances due to passive dispersal via human activities (Aubry *et al.*, 2006), they have limited active dispersal abilities (Grimm and Schaumberger, 2002 ; Honek and Martinkova, 2011). Thus, their ability to escape unsuitable conditions (by moving) is likely low. Like plants, they must endure the environment in which they find themselves. Phenotypic plasticity should thus be an important mechanism by which they respond to habitat disturbance. Particularly, it may have favoured *A. subfuscus* s.l. invasion success in logged forests by allowing it to maintain its fitness despite the reduced soil moisture content (Jack-of-all-trades scenario, Richards *et al.*, 2006). At the same time, gastropods may compete for refuges or food resources through direct (i.e., via aggressive interactions: Rollo and Wellington, 1979) or indirect interference competition (i.e., via mucus trail: Cameron and Carter, 1979 ; O'Hanlon *et al.*, 2020). Furthermore, *A. subfuscus* s.l. is very aggressive towards both conspecifics and heterospecifics and may bite almost every slug it encounters (Rollo and Wellington 1979). Thus, interference competition is also expected to play a key role in its invasion success. More specifically, *A. subfuscus* s.l. may threaten native sympatric Philomycid slugs, such as *Philomycus carolinianus* which was assessed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2019). Although it is currently unclear if *A. subfuscus* s.l. competes with *P. carolinianus* (Paustian and Barbosa, 2012), they often co-occur in North American forests (Chichester and Getz, 1969 ; Paustian, 2010) and share resources such as food or microhabitat (Paustian and Barbosa, 2012). *A. subfuscus* s.l. and Philomycid slugs thus represents a good model to determine if phenotypic plasticity and competition (i.e., by interference in our study system) interact with habitat disturbance to favour the invasion success of alien animal species.

We performed laboratory experiments to first investigate the behavioural responses of the invasive alien slug species complex, *Arion subfuscus* s.l. (hereafter *Arion*), and sympatric native species, *Philomycus* spp. (hereafter *Philomycus*), to habitat disturbance (i.e., logging) simulated by a decrease in soil moisture content. In accordance with the ideal weed and phenotypic plasticity hypotheses, we aimed to determine if *Arion* has an overall advantageous behavioural phenotype (i.e., population-level analysis) or greater phenotypic plasticity (i.e., individual-level analysis) compared to *Philomycus* in response to changes in the soil moisture content (objective 1). We chose to focus on boldness and activity-exploratory behaviours, two fitness-related traits in animals (Réale *et al.*, 2007) that may play a role in successful animal invasions (Chapple *et al.*, 2012). We also aimed to determine if *Arion* has a greater ability to compete by interference than *Philomycus* (objective 2) by investigating whether there is a shift of *Philomycus*' behaviours (locomotor, feeding, resting, and refuge use behaviours, i.e., the main behaviours of slugs; Grimm and Schaumberger, 2002 ; Rollo, 1983) in the presence of *Arion*. Moreover, if *Arion* is more aggressive towards heterospecifics than conspecifics, we would also expect the encounters between individuals to be more frequent when *Arion* is in the presence of *Philomycus* than in the presence of a conspecific. Indeed, the number of encounters represents the opportunities during which aggressions are possible (aggressive encounters happen when two slugs came within 3–8 cm of another, Rollo and Wellington, 1979).

3.4 Materials and methods

3.4.1 Experimental slug and holding conditions

During the summer of 2019, we collected *Arion* and *Philomycus* by hand within a 50-m radius circle in an unlogged temperate deciduous forest in the province of Quebec in southeastern Canada (46° 06’ N, 75° 08’ W). The canopy cover is dominated by sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.) (Nolet *et al.*, 2015). Slugs were individually held in clear plastic containers (4 × 4 × 3 cm) with wet soil litter collected near the individual to act as a refuge and prevent desiccation. Upon arrival in the laboratory (i.e., around two hours after individuals were collected), we weighed each slug (Ohaus Scout SKX123, precision ± 1 mg) and individually held them in larger clear plastic containers (20 × 15 × 10 cm) in a temperature-controlled room set at 18 °C under a 16 h light:8 h dark regime (“sunrise” at 5 a.m. and “sunset” at 9 p.m. simulating summer light conditions in southern Quebec). Each container had a thin layer of wet soil litter and *ad libitum* fresh food (i.e., half of a white mushroom). We minimised the time the slugs spent under controlled conditions by collecting them in the morning (between 6 a.m. and 8 a.m.) and by starting the experiments on the same evening. After the experiment, each slug was frozen to death to be used in a companion project in chemical ecology.

3.4.2 Experimental setup and protocol

Two separate experiments (run by the same experimenter; A.M.) were performed to achieve the two objectives of the study.

Objective 1 – In the first experiment, we evaluated the activity-exploratory and boldness behaviour (see Descriptors of slug behaviour section) of 36 *Arion* and 36 *Philomycus* in two soil moisture conditions. This experiment took place in eight arenas

(33 × 54 × 15 cm) made of a white plastic sheet with a 3-cm-thick layer of low or high moisture organic black topsoil (Unijardin brand) on the bottom. The low soil moisture condition was reached by drying the organic black topsoil for 36 hours in an incubator at 80 °C. We mixed the soil every 10 hours to make sure that it dried homogeneously. For the high soil moisture condition, we added 1.2 L of distilled water to 2.8 kg of the dried black topsoil to almost saturate it with water. The black topsoil was surrounded by a 3-cm-wide-layer of dry wood ash surrounding the arena, and a salt-covered double-sided tape was fixed on the sidewall of the arena, to serve as a fence and prevent slugs from escaping (Figure 3.1a). An artificial refuge (9 × 6 cm of black plastic sheet) was placed on the soil surface in the arena at 6 cm and 12 cm from the arena edges (Figure 3.1a).

This experiment was composed of two 12-hour trials ran during two consecutive nights. Slugs being essentially nocturnal (Grimm and Schaumberger, 2002 ; Hommay *et al.*, 1998), the two trials started twenty minutes before the "sunset" (i.e., at 8:40 p.m.) and stopped at 8:40 a.m. the next morning. Forty minutes before the beginning of each trial (i.e., at 8:00 p.m.), we randomly selected four arenas and filled them with a layer of the low soil moisture condition, and the other four arenas were filled with the high soil moisture condition. We placed fresh food (a slice of courgette and a quarter of porcini mushroom) at 33 cm from the refuge (Figure 3.1a) in amounts sufficient to constitute an *ad libitum* source and prevent interactions through exploitative competition. At 8:40 p.m., we carefully took each experimental slug (four *Arion* and four *Philomycus*) from their container and disposed them underneath the refuge of a randomly chosen arena, facing the food source. This handling lasted about 10 seconds and was kept equivalent among individuals. For each species, four individuals were randomly assigned to the low (n = 2) and the high (n = 2) soil moisture conditions in the first trial. For the second trial, the same eight individuals were used and assigned to the soil moisture condition not experienced in the first trial. Thus, each slug was exposed to the low and high soil moisture content conditions, but in random order. Between each trial, slugs were sprayed with distilled water to avoid desiccation and put back in their container in which we replaced the half of a fresh white mushroom with a new one. Topsoil and food in the arenas were replaced between each trial and the arenas were cleaned with distilled water to minimise the exposure of slugs to any potential chemical cues left by the slug during the previous trial. We replicated this experiment (composed of two consecutive trials) nine times for a total of 36 *Arion* (mean body mass ± SE: 0.96 ± 0.04 g) and 36 *Philomycus* (mean body mass ± SE: 2.36 ± 0.07 g) tested in the two soil moisture conditions (4 individuals/species/replicate x 9 replicates).

Objective 2 – In the second experiment, we investigated whether there was a shift of *Philomycus* behaviour (locomotor, feeding, resting, and refuge use behaviours, as well as the number of encounters between individuals, see *Descriptors of slug behaviour* section) in the presence of *Arion*. This experiment took place in four arenas (34 × 29 × 15 cm) made of white plastic sheets. As in the first experiment, each arena was filled with a layer of black topsoil surrounded by a layer of dry wood ash and a salt-covered double-sided tape fixed on the sidewalls. Two artificial refuges (6 × 6 cm of a black plastic sheet) were placed in the top left and bottom right corner of the arenas, at 3 cm from the edges (Figure 3.1b). These refuges were large enough to be occupied by two slugs at the same time and were therefore not a limiting resource (i.e., no exploitative competition for refuge). One hour before the “sunset”, we filled the arenas with a 3-cm-thick-layer of the high soil moisture condition (see description above). The *ad libitum* food source (a slice of courgette and a quarter of porcini mushroom) was placed in a manner that it was four times closer to the top left corner refuge than the bottom right corner refuge (Figure 3.1b). When given the choice of refuge, slugs that are superior competitors (e.g., more efficient use of the resources or more aggressive) usually choose the closest refuge from their food source (Rollo and Wellington, 1979). Twenty minutes before the “sunset” (i.e., 8:40 p.m.), we carefully took each experimental slug (four *Arion* and four *Philomycus*) from its container (handling was similar to the previous experiments) and randomly assigned it to one of the four arenas.

All individuals were distinct from those used in the first experiment. Slugs were placed on the soil surface in the middle of the arena facing the bottom left corner. Two individuals were placed in each arena according to three configurations of species pair: *Arion-Arion* (one arena), *Philomycus-Philomycus* (one arena), and *Arion-Philomycus* (two arenas). These configurations allowed us to determine if the two species may compete through interference by comparing their behaviours between heterospecific (*Arion-Philomycus*) and conspecific pairs (*Arion-Arion* or *Philomycus-Philomycus*). The focus of this study being on interspecific competition, individuals in conspecific pairs had similar body size (i.e., the difference in body size between the individuals was not higher than 35% of the body mass of the larger individual) to limit intraspecific competition (in gastropods, the body mass strongly influences the occurrence of agonistic behaviours between individuals, Rollo and Wellington, 1979). Pairs of slugs stayed 48 hours in the arena, where the first 24 hours (day 1) were considered as an acclimation period to the new conditions. We replicated this experiment 10 times to have 20 individuals tested per species and configuration of species pair (for a total of 40 *Arion*: mean body mass ± SE: 0.92 ± 0.05 g, and 40 *Philomycus*: mean body mass ± SE: 2.44 ± 0.10 g).

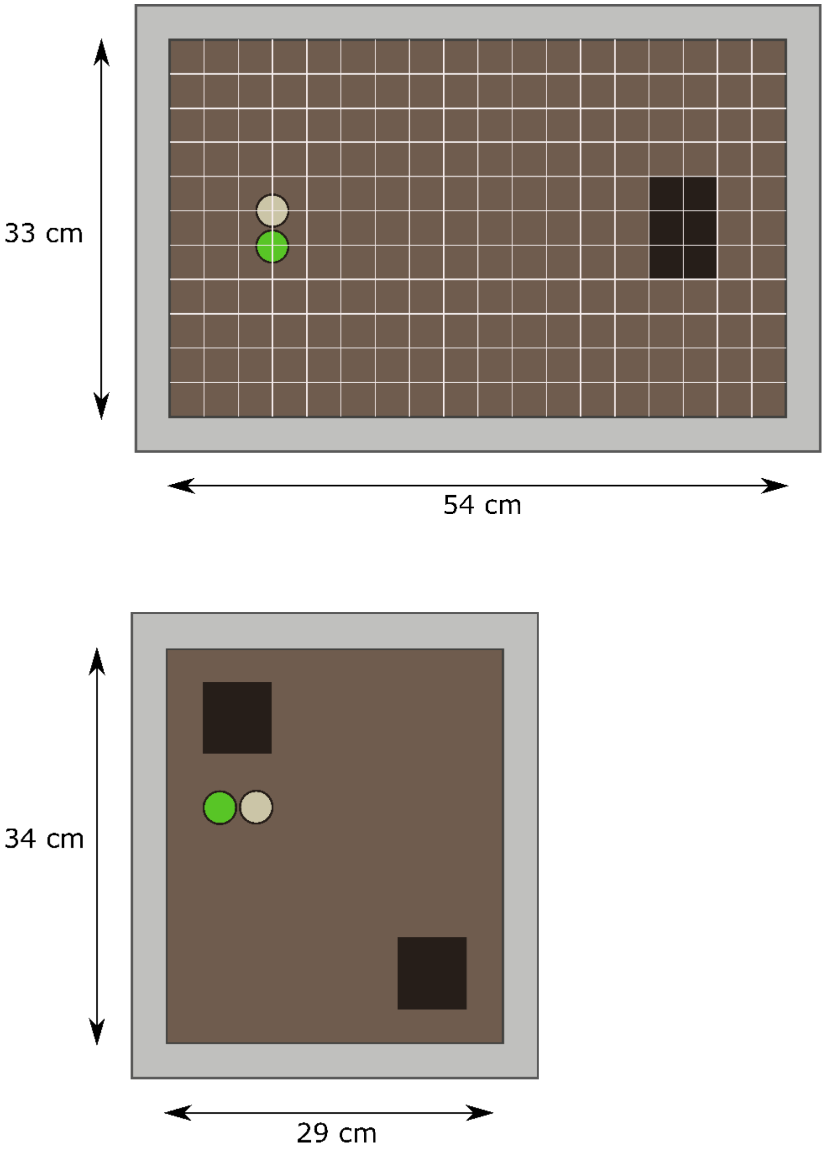

Figure 3.1: a : Arena for the assessment of boldness and activity-exploratory levels of slugs (33 × 54 × 15 cm) containing a single refuge (9 × 6 cm of black plastic sheet). To evaluate the activity-exploratory behaviour, we divided the arena into a grid of 198 equal-sized squares (3 × 3 cm) using the ImageJ program (Schneider *et al.* 2012). b: Arena for the assessment of interference competition (34 × 29 × 15 cm) containing two refuges (6 × 6 cm of black plastic sheet). The refuge in the top left corner is four-time closer to the food source than the refuge in the bottom right corner. Both arenas (a,b) were surrounded by a 3-cm-wide-layer of dry wood ash (grey area) and contained two fresh food resources *ad libitum* (green: a slice of courgette and beige: a quarter of porcini mushroom)

3.4.3 Descriptors of slug behaviour

To estimate slugs’ behaviours in both experiments, every trial was photo recorded (one picture per minute) using cameras (Wingscapes TimelapseCam Pro) suspended over the arenas. In the first experiment, as in other studies on animals, we assume that the latency to emerge from a refuge into a novel environment after a disturbance (here, keeping the slug during 10 s between fingers) was an estimate of boldness (e.g., Bridger *et al.*, 2015) and provides a measure of the willingness to take risks (Briffa *et al.*, 2013 ; Wilson *et al.*, 2010). To characterise the boldness behaviour, we evaluated the latency (minutes) to emerge from the refuge from the moment the slug was placed underneath it. Refuge emergence occurred when one-third of the slug body length was outside the refuge and the individual was moving out from the refuge. To estimate the activity-exploratory behaviour of slugs, we divided the arena into a grid of 198 equal-sized squares (3 × 3 cm) using the ImageJ program (Schneider *et al.*, 2012; Figure 3.1a). The activity-exploratory behaviour was calculated as the number of lines a slug crossed during one hour (i.e., 61 pictures) from the moment the slug started to emerge from the refuge. If during this one hour, an individual touched the ash layer or salt and quickly stopped moving for more than 10 minutes, the experiment was considered unreliable due to an extreme reaction of the individual to these dehydrating substances and the data for this individual (in both soil moisture conditions) discarded from the analyses (10 out of the 72 individuals, 2 *Arion* and 8 *Philomycus*). If an individual did not extremely react to these contacts with the ash layer or salt (i.e., stopped moving for less than 10 minutes), we discarded the photos where it was in contact with the dehydrating substances and extended its monitoring to have 61 “usable” pictures, i.e., to equalise the monitoring period among individuals (31 out of the 72 individuals, 10 *Arion* and 21 *Philomycus*). We first attempted to compare the plasticity of boldness and activity-exploratory behaviours using the reaction norm of each individual to soil moisture conditions with random regression models (Dingemanse *et al.*, 2010). However, these models failed to converge. Plasticity was then calculated as follows: (maximum trait value – minimum trait value)/(maximum trait value) modified from Valladares *et al.*(2006). This plasticity index ranges from 0 (no plasticity) to 1 (maximal plasticity). As we calculated this index only for the individuals that emerged from the refuge in both soil moisture conditions (i.e., minimum trait value > 0), it could not be equal to 1.

In the second experiment, the occurrence of three types of behavioural activities (locomotor, feeding, and resting activities) was evaluated in 30-minute intervals during the second period of 24 hours (i.e., from 9 p.m. on day 2 to 9 p.m. on day 3). Locomotor and feeding activities were defined as any movement from one place to another and food inspection with biting, respectively. Slugs not moving for more than 10 consecutive minutes were considered as resting. We also estimated the refuge use pattern by recording the position of the refuge used by the slug (i.e., close or far from the food resources) and whether it was occupied or not by the other slug when the focal slug enters the refuge. Finally, we quantified the number of encounters between pairs of individuals in each arena by counting the number of events where the two individuals were less than 5 cm apart from each other.

3.4.4 Statistical analysis

Does Arion have higher boldness and active-exploratory levels (population-level analysis) or greater behavioural plasticity (individual-level analysis) than Philomycus? (objective 1)

Population-level analysis – To determine if *Arion* was bolder than *Philomycus*, we used a Cox mixed-effect proportional hazards model. Data were right-censored (i.e., scored as incomplete) when the slug did not emerge from the refuge during the 12-hour trial (i.e., 15 out of the 66 trials for *Arion* and 6 out of the 68 trials for *Philomycus*). We included the species identity (two-level categorical variable: *Arion* and *Philomycus*) and the soil moisture condition (two-level categorical variable: low and high) as fixed effects. We also included the interaction term between these two variables because *Arion* might be bolder than *Philomycus* mainly in the low soil moisture condition, what would explain *Arion* invasion success in disturbed habitats such as logged stands. The slug identity nested within the replicate number was included as a random effect to account for non-independence arising from the two repeated observations on the same individual and same replicate observations. The soil moisture conditions order (i.e., high–low or low–high) was also added as a random effect since it could influence the behavioural response of individuals (Briffa *et al.*, 2013). Data from three *Arion* and two *Philomycus* were unusable because the camera malfunction, the slug escaped from the arena or died during the trial. Thus, this analysis was based on data from 33 *Arion* and 34 *Philomycus* (n = 134).

To determine if *Arion* was more active-exploratory than *Philomycus*, we used a Gaussian linear mixed model. The same fixed and random effects as in the boldness model were included in this analysis. We analysed data for individuals that emerged from the refuge in both soil moisture conditions and did not escape or had an extreme response to the ash layer or salt in any of them (n = 72, 16 *Arion* and 20 *Philomycus*).

Individual-level analysis (phenotypic plasticity) – To determine if *Arion* has a greater plasticity in response to soil moisture content than *Philomycus* in terms of boldness (n = 47, 19 *Arion* and 27 *Philomycus*) and activity-exploratory behaviours (n = 36, 16 *Arion* and 20 *Philomycus*), we analysed the two plasticity indices using a generalised linear mixed model with a beta distribution (which is adapted for continuous data ranging between 0 and 1) and a linear mixed model, respectively. We included the species identity as a fixed effect, and the replicate of the experiment and the soil moisture condition order as crossed random effects.

In all these analyses (both population and individual-level responses), we initially included the body mass of the slug as a covariate because it could have influenced the boldness and activity-exploratory behaviours (Honek and Martinkova, 2011). However, since the effect of body mass was not significant, and that these analyses yield similar qualitative results to the analyses that did not include it, we removed the body mass from the analyses in accordance with the principle of parsimony.

Does Arion have a greater ability to compete by interference than Philomycus? (objective 2)

In a first step, we compared several behavioural aspects (i.e., frequency of occurrence of locomotor, feeding, and resting activities, the pattern of refuge use, the temporal pattern of locomotor activity, and the number of encounters between individuals) between species in the absence of their potential competitor (i.e., comparison between conspecific pairs: *Arion-Arion* versus *Philomycus-Philomycus*) to characterise behavioural differences (if any) between the two species. To do so, the frequency of occurrence of the three main types of behavioural activities (three-level categorical variables: locomotor, feeding, and resting activities), as well as the frequency of refuge use that occurs under the farthest and closest refuge from the food source with no refuge occupancy distinction (i.e., refuge already occupied or not by an individual), were compared between conspecific pairs (i.e., *Arion-Arion* versus *Philomycus-Philomycus*) with chi-square tests. P-values were adjusted with a Holm-Bonferroni correction to counteract problems of multiple comparisons. Regarding interspecific differences in the temporal pattern of activities, we focused only on the locomotor activity given that temporal patterns of locomotor and feeding activities within each species were similar (Figure S3.1), and the resting activity is not a behaviour suspected to play a role in the invasion success of alien species (Chapple *et al.*, 2012). To do so, we estimated the overlap index (Dhat4 index, since the two investigated species had over 50 records; Rpackage *Overlap*: Ridout and Linkie, 2009) of *Arion* and *Philomycus* smoothed curves of activity produced with Kernel density functions, a non-parametric method for estimating the probability density function of a distribution of records. The overlap index is defined as the proportion of the area under the curve that is superimposed between the two activity temporal patterns of activity and ranges from 0 (no overlap between the temporal patterns of *Arion* and *Philomycus*) to 1 (complete overlap). We used bootstrapping (10 000 bootstrap samples) to estimate a 95% confidence interval around this overlap index and the “CompareCkern” function (Rpackage *activity*: Rowcliffe, 2019) to test for significance. “CompareCkern” creates a null distribution from the combined data and uses it to estimate the probability ($P < 0.05$) that the observed overlap arose by chance.

Then, for each species, we compared its behaviour in the absence and the presence of its potential competitor (i.e., comparison between conspecific and heterospecific pairs), to determine whether the presence of *Arion* altered *Philomycus* behaviours (comparison 1: *Arion-Philomycus* versus *Philomycus-Philomycus*) and vice versa (comparison 2: *Arion-Philomycus* versus *Arion-Arion*) which might be the result of interference competition. Our reasoning is that if the first comparison is verified but not the second, it would support the hypothesis that *Arion* is a superior competitor compared to *Philomycus*. To do so, we used the same statistical methods as in the first step to compare for each species i) the frequency of occurrence of the three main types of behavioural activities, ii) the frequency of refuge use that occurs under the farthest and closest refuge from the food source with no refuge occupancy distinction, iii) the frequency of refuge use that occurs when the refuge was already occupied or not by an individual with no refuge position distinction (i.e., far or close from the food source) (chi-square tests or Fisher’s exact tests), and iv) the temporal pattern of locomotor activity (the overlap index and its significance), in the absence and the presence of the potential competitor (i.e., comparison between conspecific and heterospecific pairs).

Finally, to determine if the encounters between individuals were more frequent when *Arion* is in presence of *Philomycus* (i.e., heterospecific arenas) than in presence of a conspecific (*Arion* conspecific arenas) ($n = 40$), we used a generalised linear mixed model with a Poisson distribution, which is adapted to count data with no overdispersion. We included the configuration of the species pair as a fixed effect (three-level categorical variable: *Arion-Arion* [reference level], *Philomycus-Philomycus*, and *Arion-Philomycus*) and the replicate number as a random effect.

All statistical analyses were conducted in R v. 3.6.3 (R Core Team, 2020) using the packages *coxme* (Cox mixed-effect proportional hazards model, Therneau, 2020) and *glmmTMB* for the linear and generalised linear mixed models (Brooks *et al.*, 2017).

3.5 Results

3.5.1 Does *Arion* have higher boldness and activity-exploratory levels (population-level analysis) or greater behavioural plasticity (individual-level analysis) than *Philomycus*? (objective 1)

Arion had neither higher plasticity, nor boldness and activity-exploratory levels than *Philomycus*. *Arion* was less bold than *Philomycus* at the high soil moisture condition ($\beta \pm$ SE: -1.68 ± 0.31, $P < 0.001$, Figure 3.2a) but as bold as *Philomycus* at the low soil moisture condition (significant interaction species × soil moisture condition: $\beta \pm$ SE: 1.35 ± 0.42, $P < 0.010$; Figure 3.2a). Moreover, *Arion* was less plastic in terms of boldness than *Philomycus* (observed plasticity index: 0.58 ± 0.04 for *Philomycus* versus 0.33 ± 0.05 for *Arion*, $P < 0.001$, Figure 3.2b).

As for the activity-exploratory behaviour, there were no interspecific differences regardless of the soil moisture condition (Figure 3.3, Table 3.1) and *Arion* was as plastic as *Philomycus* (observed plasticity index: 0.44 ± 0.08 for *Arion*, 0.50 ± 0.07 for *Philomycus*, $P = 0.584$, Figure 3.3).

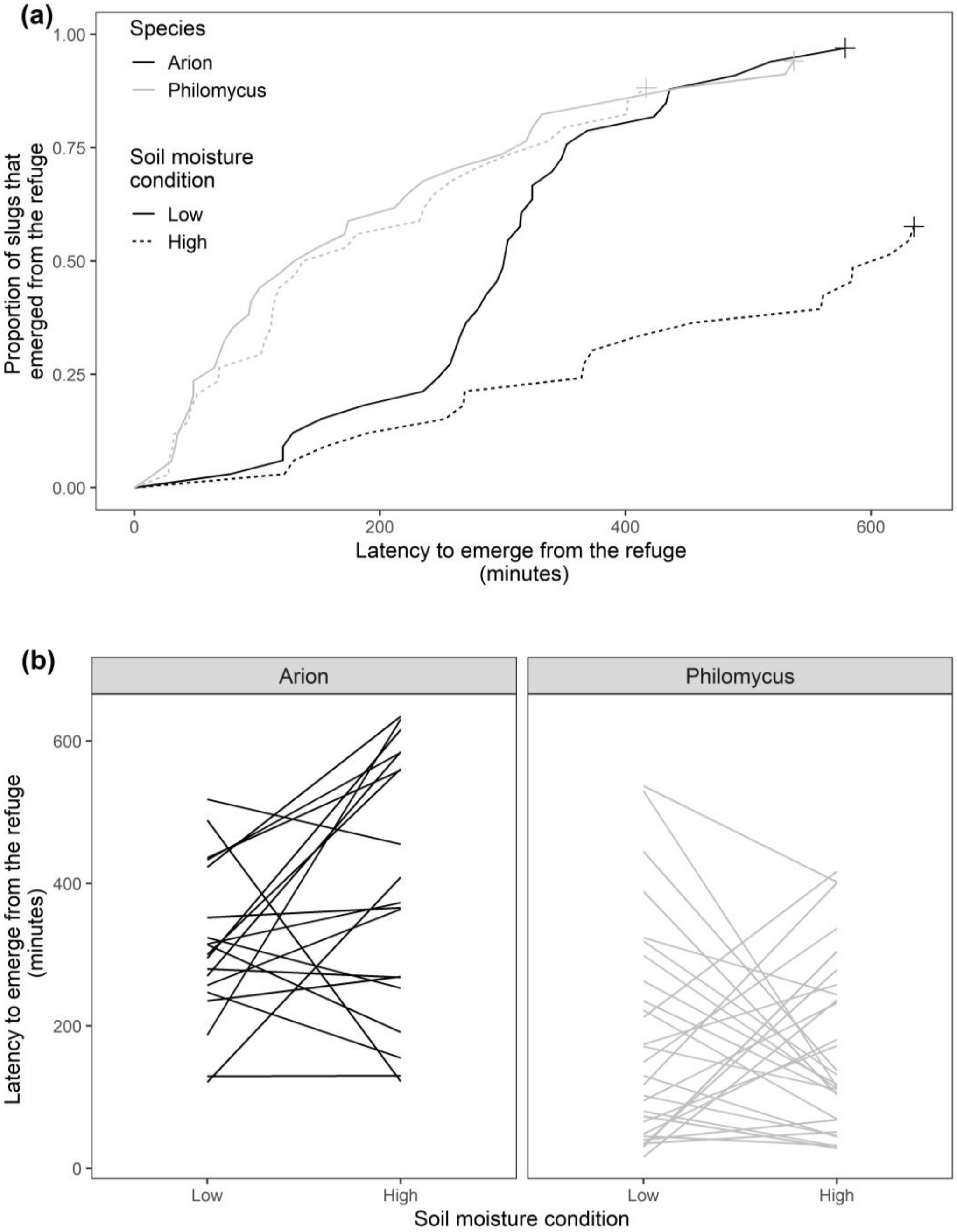

Figure 3.2: (a) Proportion of *Arion* (black line) and *Philomycus* (gray line) that emerged from the refuge in the low (dotted line) and the high (solid line) soil moisture condition in function of the latency to emerge from the refuge (minutes). The symbol at the end of the curve corresponds to the proportion of individuals that emerged from the refuge at the end of the 12-hour trial (i.e., after 720 min). (b) Latency to emerge from the refuge (minutes) for *Arion* and *Philomycus* individuals in the low and high soil moisture conditions. Each line represents the difference in the response of one individual to the two soil moisture conditions (i.e., reaction norm of each individual)

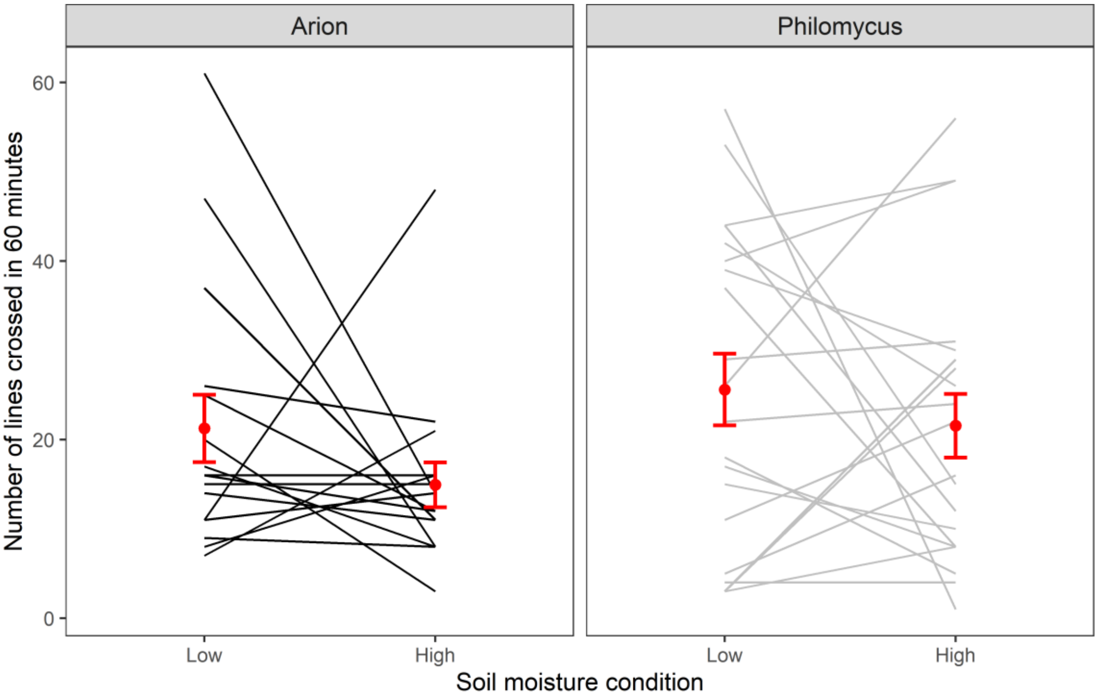

Figure 3.3: Mean population activity-exploratory behaviour (i.e., the number of lines crossed in 60 minutes) for *Arion* and *Philomycus* in the low and high soil moisture conditions (red circle). Error bars represent standard errors. The reaction norm of each individual is represented by a single line

Table 3.1: Generalised linear mixed model describing the effect of the species, soil moisture condition and their interaction on the population activity-exploratory

Predictors	**Log-Mean**	**std. Error**	**Z-value**	**P-Value**
Intercept	2.69	0.19	14.22	**<0.001**
Species [Philomycus]	0.37	0.24	1.56	0.118
Soil moisture condition [low]	0.33	0.25	1.34	0.180
Species [Philomycus] * Soil moisture condition [low]	-0.17	0.33	-0.51	0.608

3.5.2 Does *Arion* have a greater ability to compete by interference than *Philomycus*?

In the absence of their potential competitor (i.e., comparison between conspecific pairs), *Arion* and *Philomycus* behaviour differed in the frequency of occurrence of locomotor, feeding and resting activities ($\chi2 = 80.54$, df = 2, $P < 0.001$, Figure 3.4a) and in their temporal pattern of locomotor activity (overlap = 0.71, $P < 0.001$, Figure 3.4b). *Arion* moved and rested less frequently than *Philomycus* (locomotor activity: 17% vs 22%, $\chi2 = 9.02$, df = 1, $P < 0.010$; resting activity: 63% vs 71%, $\chi2 = 15.20$, df = 1, $P < 0.001$), but fed almost three times more frequently than *Philomycus* (20% vs 7%, $\chi2 = 77.67$, df = 1, $P < 0.001$, Figure 3.4a). Regarding the temporal pattern of locomotor activity, *Philomycus* and *Arion* were mainly active at night, but *Arion* was more active during the daylight hours than *Philomycus* (overlap = 0.71, $P < 0.001$, Figure 3.4b). As for the pattern of refuge use, *Arion* used more frequently the closest refuge from the food source (i.e., 90% of the observations) compared to *Philomycus* ($\chi2 = 17.15$, df = 1, $P < 0.001$, Figure 3.4c). Indeed, *Philomycus* used almost as frequently the farthest (55%) and the closest (45%) refuge from the food source.

The presence of the potential competitor (i.e., comparison between conspecific and heterospecific pairs) did not affect the frequency of occurrence of the three types of behavioural activities of both species (*Arion* ; $\chi2 = 4.24$, df = 2, $P = 0.120$, Figure 3.5a; *Philomycus*: $\chi2 = 3.24$, df = 2, $P = 0.198$, Figure 3.5b), their temporal pattern of locomotor activity (*Arion*: overlap = 0.878, $P = 0.316$, Figure 3.5c; *Philomycus*: overlap = 0.91, $P = 0.260$, Figure 3.5d), and their pattern of refuge use. In both species, the frequency of refuge use that occurs under the farthest and the closest refuge from food source (i.e., far versus close with no distinction for refuge occupancy, *Arion*: Fisher exact test: $P = 1$, Figure 3.5e; *Philomycus*: $\chi2 = 1.12$, df = 1, $P = 0.864$, Figure 3.5f) and when the refuge was already occupied or not by an individual (i.e., occupied versus unoccupied with no distinction for refuge position, *Arion*: $\chi2 = 0.58$, df =1, $P = 0.886$,

Figure 3.5e; *Philomycus*: $\chi 2$ = 3.17, df =1, P = 0.300, Figure 3.5f) did not differ regardless of the presence of a potential competitor or not. Finally, the number of encounters between individuals was similar whether *Arion* and *Philomycus* were in the absence (i.e., comparison between conspecific pairs, β ± SE: -0.23 ± 0.19, P = 0.240) or in the presence of the other species (i.e., comparison between conspecific and heterospecific pairs for *Arion*: β ± SE: -0.26 ± 0.17, P = 0.116 and *Philomycus*: β ± SE: 0.03 ± 0.18, P = 0.855).

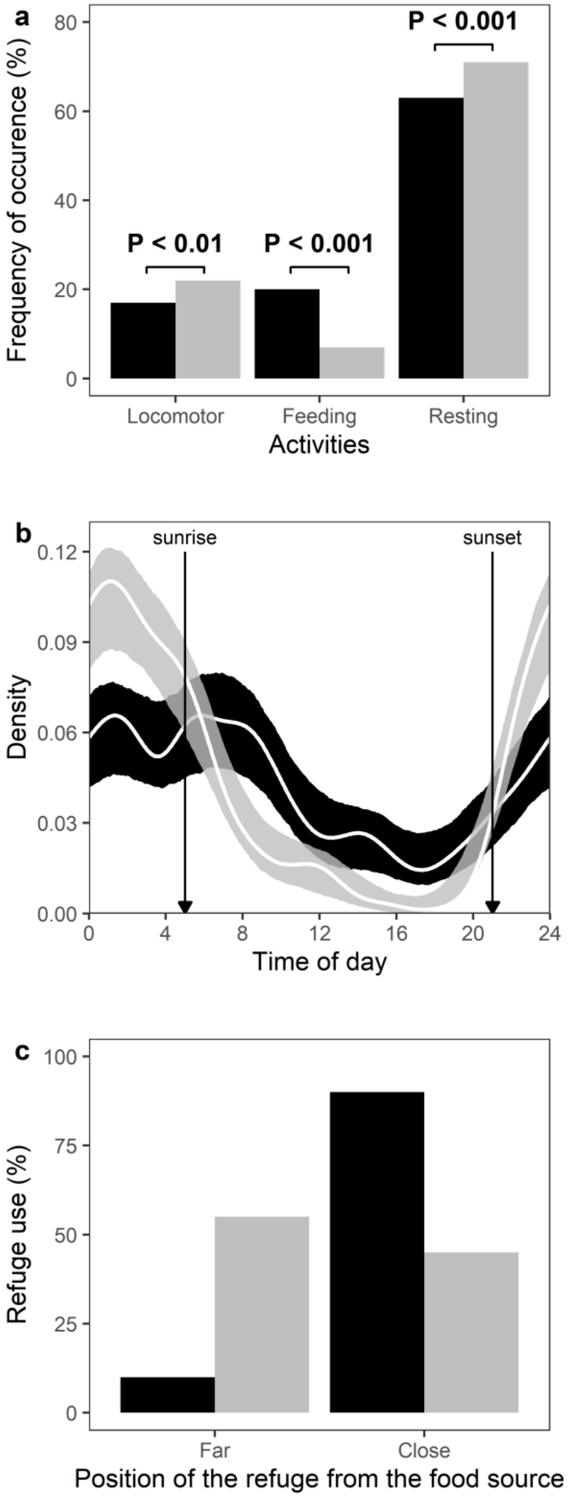

Figure 3.4: (a) Frequency of occurrence (%) of locomotor, feeding and resting activities, (b) temporal pattern of locomotor activity, and (c) refuge use pattern (%) for *Arion* (black) and *Philomycus* (grey) in conspecific pairs

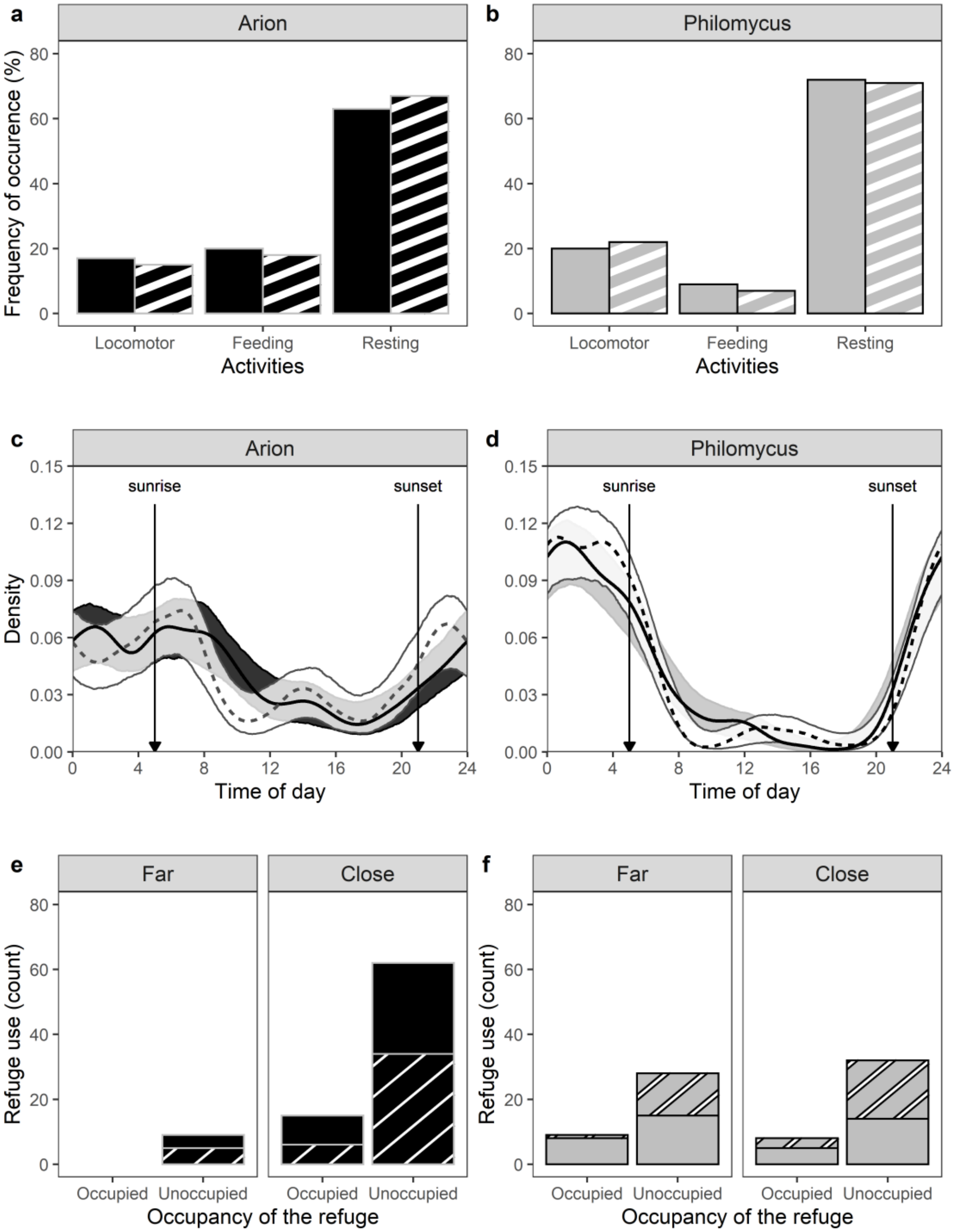

Figure 3.5: Frequency of occurrence (%) of locomotor, feeding and resting activities (a, b), the temporal pattern of locomotor activity (c, d), and refuge use pattern (count) for the farthest and closest refuge from food source (e, f) for *Arion* (a, c, e) and *Philomycus* (b, d, f) in the absence (i.e., conspecific pairs, solid bar and line, and coloured shaded area) or in the presence of their competitor (i.e., heterospecific pairs, hatched bar, dotted line, and white shaded area)

3.6 Discussion

Our findings show that the invasion success of *A. subfuscus* s.l. in disturbed habitats is unlikely to be the result of greater phenotypic plasticity or more advantageous trait values than native *Philomycus* spp. in terms of boldness and activity-exploratory behaviour. These findings support neither the plasticity hypothesis (Baker, 1965 ; Richards *et al.*, 2006) nor the ideal weed hypothesis (Baker, 1965 ; Colautti *et al.*, 2014). Our results also suggest that interference competition between the two species is unlikely to have played a role in *Arion* invasion success in disturbed habitats and be a driver of native species decline (see chapter II) since the behaviour (i.e., locomotor, feeding, resting, and refuge use) of neither *Philomycus* nor *Arion* were affected by the presence of the other species. However, the more advantageous refuge use pattern and feeding behaviour of *Arion* could provide it with a competitive advantage and tend to support the ideal weed hypothesis.

To our knowledge, this study is one of the first to evaluate the phenotypic plasticity hypothesis in animal species by comparing the plasticity of invasive alien animal species to that of a native species. Our results showed that *Arion* did not have greater phenotypic plasticity in boldness and activity-exploratory behaviour than *Philomycus*, thus not supporting the plasticity hypothesis. Other studies comparing the plasticity of alien to native animal species are rare but are consistent with our findings. Indeed, Chown *et al.* (2007) and Phillips *et al.* (2020) have shown, based on thermal minima, maxima and range, on resistance to desiccation and rate of egg development, that invasive alien invertebrate species did not have greater plasticity than native ones in response to changes in temperature. This finding contrasts with plants for which greater plasticity in alien compared to native species has been often observed (e.g., Davidson *et al.*, 2011 ; Funk, 2008 ; Torchyk and Jeschke, 2018). Unlike most animals, plants are essentially sessile organisms and cannot escape unfavourable environments through movement. They may thus have evolved to cope with a wider range of environmental conditions and exhibit greater phenotypic plasticity than animal species (Borges, 2008 ; Bradshaw, 1965). However, greater numbers of traits and invasive alien species need to be examined before dismissing the phenotypic plasticity hypothesis as a mechanism promoting the invasion success of alien animal species in disturbed habitats. Other traits that we did not measure in this study might indeed play a major role in *Arion* invasion success in disturbed habitats (e.g., antipredator or oviposition behaviours, Chapple *et al.*, 2012 ; Poidatz *et al.*, 2018). Furthermore, trait plasticity is context-dependent (Hulme and Bernard-Verdier, 2018) and its assessment along a gradient may differ from another one and may lead to different interpretations depending on which conditions it has been evaluated (Hulme, 2008). Thus, studying the behavioural response to other environmental variables affected by logging (e.g., temperature or food supply) would be necessary.

Otherwise, although *Arion* was not more plastic in its boldness than *Philomycus*, its mean population boldness was higher in the low than in the high soil moisture condition (while it was similar for *Philomycus* in both soil moisture conditions). This result highlights an essential component of the plasticity that is rarely considered in studies, the direction of trait value change. Since boldness can correlate with activity, dispersion and exploration tendencies (Cote *et al.*, 2010 ; Dahirel *et al.*, 2017 ; Monceau *et al.*, 2015), bolder *Arion* in logged habitats (i.e., in low soil moisture condition) may cover more ground, accumulate information more rapidly, and make more frequent food discoveries, which may favour its fitness and invasion success in logged habitats compared to unlogged habitats. Similarly, Chown *et al.* (2007) showed that invasive alien and native springtail species had similar plasticity but that warmer conditions promote survival to desiccation in the invasive species while it reduces it in the native species. Their findings suggest that phenotypic plasticity may favour invasive over native springtail species in response to climate change even though the former did not have greater phenotypic plasticity than native species. Similarly, the plasticity of *Arion* boldness behaviour may favour its invasion success, not because it is greater than

Philomycus, but because it promotes an increase in *Arion* mean population boldness in logged habitats (i.e., in low soil moisture condition).

Our findings also did not support the ideal weed hypothesis since *Arion* did not have a higher boldness or activity-exploratory behaviour than *Philomycus*. However, our results showed that *Arion* almost exclusively used the refuge closest from the food source, whereas *Philomycus* used both refuges as frequently. By selecting the refuge that reduces its required travel to access food, *Arion* fed more frequently (almost three times as often as *Philomycus*) and minimised its locomotion costs. This might be especially advantageous during summer (i.e., the main slug growth period in temperate and boreal forests) when soil moisture is low and the temperature high because of low canopy cover in logged forests (Chen *et al.*, 1993). Indeed, locomotion in terrestrial gastropods is a costly physiological investment in water (Theenhaus and Scheu, 1996). Mucus is mainly composed of water and 10–15% of the energy assimilated from food is spent on mucus production in the snail Cepaea nemoralis (Williamson and Cameron, 1976). The fact that *Arion* almost exclusively used the refuge that provides the best access to food source could thus allow it to invest more energy in reproduction (and less in locomotion), thus favouring its fitness and ultimately its invasion success. Acquiring a great amount of food to invest in a unique reproduction event is an important strategy for semelparous species like *A. subfuscus* s.l., which has a short lifespan (usually less than a year) and quickly dies after reproduction (Beyer and Saari, 1978 ; Jennings and Barkham, 1975). Such a strategy is less necessary for Philomycid species, which has a longer lifespan than *Arion* and does not die after reproduction (A. Mazaleyrat and A. Dupuch, personal observation). Thus, even though our second experiment did not intend to test the ideal weed hypothesis, our findings tend to support it, in a way that *Arion* would better exploit the resources than *Philomycus*.

The role of interference competition in *Arion* invasion success also seems limited. Our results indicate that the two species differ in their frequency of occurrence of locomotor, feeding and resting activities, in their temporal pattern of locomotor activity, and their refuge use pattern. Although we do not know whether these behavioural differences are large enough to enable coexistence between these species, we did not witness any change in the behaviour of *Philomycus* or *Arion* in the presence of a heterospecific. This is unexpected, given that *A. subfuscus* s.l. is very aggressive towards other slug species (including species twice its size, Rollo and Wellington, 1979), but consistent with Paustian (2010) that did not find any evidence of interspecific interference competition. The lack of shift in *Arion* and *Philomycus* behaviour cannot be attributed to slug density (two individuals per 0.1 m2) since it was ten times the one observed in forests (Kappes and Schilthuizen, 2014 ; see also chapter II) and twice the one in field cages used by Rollo and Wellington (1979). However, it may be possible that the high soil moisture content in the arenas may have limited the occurrence of aggressive behaviours. Indeed, agonistic behaviours in terrestrial slugs have been shown to vary seasonally and increase in dry, warm summer conditions (Rollo and Wellington, 1979).

Our experiments thus give important insights into the mechanisms that favour the invasion success of alien species in disturbed ecosystems such as logged habitats. Our findings do not support the phenotypic plasticity hypothesis or any role of interference competition in *Arion* invasion success in disturbed habitats but tend to support the ideal weed hypothesis. This study also highlights an important but understudied component of phenotypic plasticity that might favour the invasion success of alien species in disturbed habitats: the direction of the plasticity. Indeed, our results suggest that the direction of the behavioural plasticity might be more important than the magnitude of plasticity in *Arion* invasion success in logged habitats. However, more studies on various alien animal species and traits are needed to clarify the mechanisms involved in their invasion success in disturbed habitats and to accurately evaluate the role of both the direction and magnitude of plasticity, as well as the support of the ideal weed hypothesis.

3.7 Acknowledgements

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3.8 Supplementary material

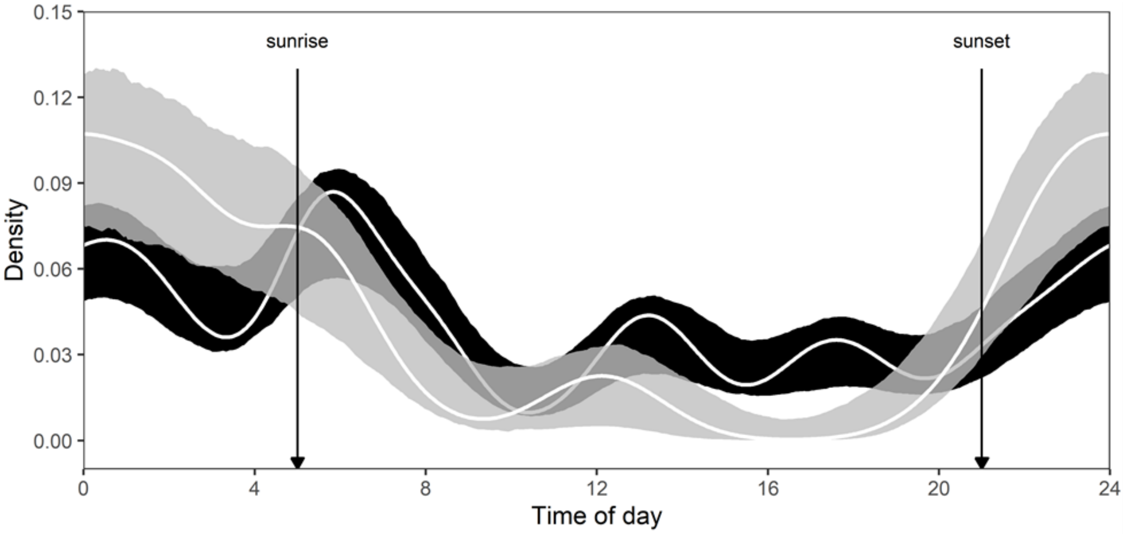

Figure S3.1: Temporal pattern of feeding activity for *Arion* (black) and *Philomycus* (grey) in conspecific pairs

CONCLUSION

La plupart des connaissances actuelles sur les mécanismes favorisant les invasions biologiques proviennent d'études portant sur les espèces exotiques végétales. Notre compréhension des mécanismes impliqués dans les invasions animales reste donc limitée, tout particulièrement dans les habitats perturbés par des activités anthropiques. Cette thèse apporte donc un regard novateur dans le domaine des invasions biologiques en s'intéressant à l'effet d'une perturbation anthropique (coupe forestière) sur le succès d'envahissement des espèces exotiques animales (*Arion*) (chapitre I et II) et le déclin des espèces indigènes animales (*Philomycus*) (chapitre II). C'est également une des rares études à s'être intéressée à certains mécanismes par lesquels les espèces exotiques profitent de la perturbation (chapitre II et III). Cette thèse aura également permis d'évaluer si l'espèce exotique animale peut représenter une menace pour le maintien des populations indigènes par le biais de la compétition par interférence (chapitre III).

4.1 Les coupes forestières, comme perturbation d'origine anthropique, favorisent-elles le succès d'envahissement d'espèces exotiques animales ?

L'effet des coupes forestières sur le succès d'envahissement des espèces exotiques a été étudié à de nombreuses reprises chez les espèces végétales (p. ex. Brown et Gurevitch, 2004 ; Chabrerie *et al.*, 2008 ; Döbert *et al.*, 2018). Chez les espèces animales, les études sont trop peu nombreuses pour permettre de conclure sur le rôle de l'exploitation forestière dans les invasions biologiques. Notre étude révèle la présence d'*Arion* dans de nombreux écosystèmes forestiers témoins ou perturbés par des coupes en Ontario et au Québec, et démontre que les coupes forestières ne favorisent pas systématiquement le succès d'envahissement d'*Arion* (chapitre I et II).

Ces résultats sont en accord avec les études existantes, majoritairement réalisées chez les espèces végétales, qui pour certaines observent une relation positive entre une perturbation et le succès d'envahissement des espèces exotiques (Alston et Richardson, 2006 ; Altman et Whitlatch, 2007 ; Grez *et al.*, 2013), pour d'autre aucune relation (Callaham Jr *et al.*, 2003 ; Hester et Hobbs, 1992), voire une relation négative (Callaham Jr *et al.*, 2003 ; Prober *et al.*, 2009 ; Witt et Nongogo, 2011). L'hypothèse de la perturbation, selon laquelle une perturbation favoriserait le succès d'envahissement des espèces exotiques, n'est donc pas toujours supportée (Nordheimer et Jeschke, 2018).

Une explication à ce constat serait que seules les perturbations qui modifient les conditions biotiques et abiotiques de manière à promouvoir l'introduction, l'établissement ou l'expansion des espèces exotiques favoriseraient leur succès d'envahissement (Hobbs et Huenneke, 1992 ; Lozon et MacIsaac, 1997). Il a par exemple été démontré que des conditions environnementales défavorables pouvaient empêcher ou ralentir l'établissement et l'expansion d'espèces exotiques animales et végétales (Gerhardt et Collinge, 2007 ; Hawes et Parrish, 2003 ; Menke *et al.*, 2007 ; Ning *et al.*, 2019 ; Warren II *et al.*, 2020). Les caractéristiques d'une perturbation (p. ex. intensité) pourraient donc moduler son effet sur le succès d'envahissement des espèces exotiques. Nos résultats confirment cette conclusion en montrant que l'effet de la coupe sur le succès d'envahissement d'*Arion* dépendait de son intensité et du temps écoulé depuis son occurrence (chapitre I). L'effet des coupes forestières sur le succès d'envahissement d'*Arion* devra être étudié dans un plus grand nombre d'écosystèmes forestiers au Québec et en Ontario afin de déterminer plus précisément quelles intensités de coupe et combien de temps cela peut prendre après ce type de perturbation pour que cette dernière favorise le succès d'envahissement.

Dans le chapitre I, nous avons développé un cadre conceptuel de l'hypothèse de la perturbation qui prend explicitement en compte l'effet de l'intensité de la perturbation et du temps écoulé depuis son occurrence sur le succès d’envahissement des espèces exotiques, incluant la manière dont ces deux caractéristiques affectent les conditions biotiques et abiotiques de l’écosystème. Le manque de connaissances sur les conditions biotiques et abiotiques influençant le succès d’envahissement d’*Arion* ne nous ont malheureusement pas permis de tester ce cadre conceptuel. Celui-ci fournit toutefois un contexte dans lequel les prédictions concernant l'effet de la perturbation et de ses caractéristiques sur le succès d'envahissement peuvent être testées. La formulation d’un cadre conceptuel novateur apporte un éclairage nouveau sur les circonstances pour lesquelles une perturbation va favoriser les invasions biologiques mais n’identifie pas clairement les mécanismes sous-jacents impliqués, ce qui a été étudié dans les chapitre II et III.

4.2 Mécanismes associés au succès d’envahissement d’*Arion* dans les habitats perturbés par des coupes forestières

4.2.1 Rôle des modifications d’attributs de l’habitat générées par la coupe

Des études précédentes ont montré que les attributs de l'habitat sont un facteur déterminant pour expliquer les invasions végétales (Simonová et Lososová, 2008 ; Truscott *et al.*, 2007). Leur rôle dans le succès d’envahissement d’espèces exotiques animales a toutefois été peu étudié (p. ex. Kornis *et al.*, 2013 ; Nawrot *et al.*, 2015), tout particulièrement dans un contexte où ces attributs sont modifiés par des activités anthropiques (voir : Chabrerie *et al.*, 2008 ; Lembrechts *et al.*, 2016 ; Quiroz *et al.*, 2011 ; White *et al.*, 2013 pour les plantes). Nos résultats suggèrent que les modifications d’attributs de l'habitat générées par la coupe forestière ont favorisé le succès d’envahissement d’*Arion* (chapitre II). En effet, selon le site d’étude, les changements d’attributs de l’habitat semblent avoir favorisé le succès d’envahissement d’*Arion* directement, en rendant les conditions plus favorables pour ces dernières, ou indirectement, en causant le déclin de *Philomycus*, permettant à *Arion* de remplir le vide causé par ce déclin. Nos connaissances sur l'autoécologie des limaces en milieu forestier étant actuellement limitées (mais voir : COSEWIC, 2019 ; Grimm *et al.*, 2009), il est difficile d'expliquer l'effet des modifications d'attributs de l'habitat que nous avons documentés. Clarifier la relation entre les attributs de l'habitat et des indicateurs du succès d'envahissement (p. ex. abondance) pourrait permettre de déterminer si d'autres perturbations naturelles ou anthropiques sont susceptibles de favoriser le succès d'envahissement des espèces exotiques de limaces.

De plus, le fait que la modification d'attributs de l'habitat influence soit directement ou indirectement le succès d'envahissement d'*Arion* selon le site d'étude est en phase avec l'idée que le succès d'envahissement des espèces exotiques dépend souvent du contexte et est dû à une combinaison de facteurs et mécanismes (Catford *et al.*, 2009; Daehler, 2003 ; Williamson and Fitter, 1996). En accord avec nos résultats, il a été précédemment montré que les mécanismes favorisant le succès d'envahissement des espèces exotiques végétales dépendait de la localisation géographique (D'Antonio, 1993 ; Taylor *et al.*, 2016). Cependant, aucune étude (à notre connaissance) n'a démontré cela pour des espèces exotiques animales dans des forêts perturbées par des coupes. Cette thèse a également démontré l'importance d'évaluer plusieurs indicateurs du succès d'envahissement pour mieux évaluer les mécanismes associés aux invasions (Foxcroft *et al.*, 2004 ; Moore et Elmendorf, 2006 ; Rouget et Richardson, 2003 ; Truscott *et al.*, 2007). En effet, les mécanismes influençant le succès d'envahissement d'*Arion* dépendaient de l'indicateur utilisé pour quantifier le succès d'envahissement (dans ce cas, abondance ou masse corporelle).

4.2.2 Rôle des valeurs des traits comportementaux et leur plasticité

Plusieurs études ont démontré que les espèces exotiques envahissantes végétales avaient des valeurs de traits plus avantageuses (hypothèse de l'envahisseur idéal) ou une plus grande plasticité phénotypique (hypothèse de la plasticité phénotypique) que les espèces indigènes, ce qui pourrait favoriser leur succès d'envahissement dans de nouveaux habitats, tels que les habitats perturbés. Bien que certaines études aient documenté des valeurs de traits plus avantageuses chez les espèces exotiques envahissantes animales comparativement aux espèces indigènes, très peu ont porté sur la plasticité (p. ex. Chown *et al.* 2007; Phillips *et al.* 2020) et quasiment aucune sur la plasticité comportementale (Torchyk and Jeschke, 2018).

Dans le cadre de cette thèse, des expériences en milieu contrôlé ont été réalisées afin de comparer deux traits comportementaux pouvant favoriser le succès d'envahissement des espèces exotiques, l'audace et l'activité exploratoire (Chapple *et al.*, 2012), ainsi que leur plasticité chez *Arion* et *Philomycus* (chapitre III).

Nos résultats démontrent qu'*Arion* n'avait ni des niveaux d'audace et d'activité-exploratoire plus élevés, ni une plasticité dans ces comportements plus élevée que *Philomycus*. Ces résultats ne supportent donc pas l'hypothèse de la plasticité phénotypique. D'autres données récoltées dans le cadre de ces expériences ont révélé qu'*Arion* utilisait presque exclusivement le refuge le plus proche de la source de nourriture, tandis que *Philomycus* utilisait les deux refuges aussi fréquemment. Ces résultats tendent à supporter l'hypothèse de l'envahisseur idéal car *Arion* pourrait exploiter plus efficacement les ressources que *Philomycus*. En effet, en plus de choisir le refuge le plus proche de la source de nourriture, *Arion* se nourrissait également plus fréquemment que *Philomycus* (presque trois fois plus souvent). Ce comportement pourrait lui permettre de réduire ses déplacements pour accéder à la nourriture, et donc de minimiser ses coûts de locomotion liés à l'alimentation, ce qui serait particulièrement avantageux lorsque l'humidité du sol est faible et la température élevée, comme c'est souvent le cas dans les forêts exploitées ayant un faible couvert forestier (Chen *et al.*, 1993). Cette hypothèse nécessite toutefois d'être testée avant de conclure sur le caractère avantageux du comportement d'*Arion* comparativement à *Philomycus*.

De plus, bien qu'*Arion* n'ait pas exprimé une plasticité plus importante que *Philomycus*, le niveau d'audace de la population d'*Arion* était plus élevé dans les conditions de faible que de forte humidité du sol (pas de changement pour *Philomycus*). Étant donné que l'audace peut être corrélée avec l'activité, la dispersion et les tendances d'exploration (Cote *et al.*, 2010 ; Dahirel *et al.*, 2017), une espèce plus audacieuse dans une forêt coupée (c'est-à-dire dans des conditions de faible humidité du sol) pourrait accumuler des informations et découvrir des ressources alimentaires plus rapidement, ce qui pourrait favoriser son aptitude phénotypique et donc son succès d'envahissement. Ce résultat met en évidence une composante essentielle de la plasticité rarement prise en compte dans les études, soit la direction du changement de valeur des traits. Les implications de ce résultat dépassent le simple cadre de l'étude des invasions biologiques. En effet, les espèces (exotiques et indigènes) répondent aux changements de conditions environnementales (p. ex induit par une perturbation ou le réchauffement climatique) par la plasticité (p.ex. Seebacher *et al.*, 2015). Il est donc crucial de bien cerner les tenants et aboutissants de l'amplitude des changement phénotypiques observés et de leur direction pour prédire les effets de ces changements sur les espèces exotiques et indigènes

4.2.3 Rôle de la compétition interspécifique

La supériorité compétitive des espèces exotiques comparativement aux espèces indigènes peut contribuer au succès d'envahissement des espèces exotiques dans les habitats perturbés et causer le déclin des espèces indigènes (Didham *et al.*, 2007). Des expériences menées en milieu contrôlé suggèrent qu'*Arion* n'a pas une plus grande capacité de compétition par interférence que *Philomycus*, puisque le comportement de cette dernière n'était pas influencé par la présence d'*Arion*, dans un contexte où les ressources n'étaient pas limitantes (chapitre III). Toutefois, dans un contexte de ressources limitantes, le comportement d'utilisation des refuges et le comportement alimentaire d'*Arion* pourraient lui conférer un avantage compétitif en lui permettant de les exploiter plus efficacement que *Philomycus*. Il est donc possible que la relation négative observée entre l'abondance de *Philomycus* et celle d'*Arion* dans les peuplements témoins (chapitre II, Figure S2.2) soit le résultat d'une compétition par exploitation. Bien que certaines études suggèrent que la nourriture ne serait pas une ressource limitante en milieu naturel pour les gastéropodes (Boycott, 1934), les limaces peuvent, dans certaines circonstances (p.ex. sécheresses ou temps froid), être confinées dans des zones restreintes où les ressources sont limitées, ce qui favoriserait la présence de compétition, comme le soulèvent Paustian et Barbosa (2012). Ainsi, la présence de compétition par exploitation entre *Arion* et *Philomycus* nécessite d'être étudiée plus en détail et surtout dans des conditions de ressources limitées. De plus, aucune étude longitudinale de l'abondance de *Philomycus* et *Arion* n'ayant été menée à ce jour, il est difficile de déterminer si l'envahissement d'*Arion* a entrainé une diminution de l'abondance de *Philomycus*. Jusqu'à présent, les études sur les interactions entre les espèces exotiques et indigènes ont majoritairement porté sur la compétition par interférence, si bien que le rôle des interactions biotiques indirectes (p. ex. compétition par exploitation ou apparente) dans les invasions biologiques et le déclin des espèces indigènes est peu connu (White *et al.*, 2006, mais voir : Damas-Moreira *et al.*, 2020 ; Petren et Case, 1996). Des études plus approfondies sur les interactions biotiques permettront de mieux comprendre et prédire les impacts potentiels des espèces exotiques et de concevoir des stratégies de gestion appropriées pour les espèces exotiques et indigènes.

En résumé, la réalisation d'expériences en milieu contrôlé (chapitre III) combinées à des prises de données en milieu naturel (chapitre I et II) a permis d'apporter des réponses concernant les mécanismes associés au succès d'envahissement d'espèces exotiques animales dans les habitats perturbés par des coupes. Cette thèse a notamment permis de déterminer (1) que les coupes forestières peuvent favoriser le succès d'envahissement des espèces exotiques animales dépendamment de leurs caractéristiques (intensité et temps écoulé depuis la perturbation) (chapitre I), (2) que les changements d'attributs de l'habitat générés par les coupes pourraientdirectement causer le déclin des espèces indigènes (*Philomycus*) et favoriser directement ou indirectement le succès d'envahissement des espèces exotiques (*Arion*) (chapitre II), (3) que des comportements d'audace et d'activité exploratoire plus élevés ou plus plastiques ne sont pas nécessairement impliqués dans le succès d'envahissement d'une espèce exotique animale (chapitre III), et (4) que si *Arion* menace *Philomycus*, il est plus probable que ce soit par le biais de compétition par exploitation que par interférence (chapitre III). Cette thèse propose également un cadre conceptuel inédit qui peut orienter de prochaines recherches (chapitre I).

4.3 Représentativité des résultats de cette thèse

Les limaces, ainsi que de nombreuses autres espèces d'invertébrés, telles que les gastéropodes ou arthropodes, sont des modèles biologiques pertinents pour étudier les effets des coupes forestières dans les invasions biologiques animales, car ces espèces sont particulièrement sensibles aux conditions climatiques et aux attributs de l'habitat (Buddle *et al.*, 2000 ; Cameron et Leather, 2012 ; Kappes, 2005, 2006 ; Lövei et Sunderland, 1996). Si une coupe altère ces conditions environnementales, ces espèces devraient être parmi les premières à montrer une réponse mesurable. Il est attendu que le nombre d'espèces exotiques de mollusques augmente fortement d'ici 2050 (Seebens *et al.*, 2020). Puisque certaines espèces exotiques de gastéropodes causent d'importants dommages dans les écosystèmes agricoles au Canada (Grimm *et al.*, 2009), et que leur herbivorie peut influencer l'abondance et la distribution des plantes ainsi que le recrutement des semis d'arbres en milieu forestier (Joe et Daehler, 2008 ; Liang *et al.*, 2019 ; Nystrand et Granström, 2000 ; Pigot et Leather, 2008), il est important d'identifier les mécanismes favorisant leur succès d'envahissement dans ces habitats. Ces mécanismes sont susceptibles de dépendre du stade de l'envahissement (Dietz et Edwards, 2006 ; Theoharides et Dukes, 2007). *Arion* était probablement déjà présente dans la plupart des peuplements forestiers avant l'occurrence de la coupe, comme en témoigne leur présence dans de nombreux peuplements témoins (chapitre I et II). Les résultats de cette thèse s'appliquent alors surtout à des espèces exotiques animales établies (c.-à-d. qui survivent et se reproduisent dans la région d'introduction). Cette thèse s'est intéressée à l'effet des coupes sur le succès d'envahissement d'*Arion* mais d'autres types de perturbations surviennent dans les écosystèmes forestiers. En effet, les perturbations naturelles telles que les feux et les épidémies d'insectes affectent régulièrement les écosystèmes forestiers d'Amérique du Nord et la fréquence de ces perturbations pourrait augmenter au cours du siècle (Dale *et al.,* 2001 ; Seidl *et al.,* 2017). Les environnements créés par ces deux types de perturbations (feu et coupe) peuvent différer en termes de structure de sol, couverture des arbustes, des mousses et lichens, des débris ligneux, des plantes vasculaires et de l'ouverture de la canopée (Hart et Chen, 2008 ; Larrivée *et al.,* 2005 ; Nguyen-Xuan *et al.,* 2000 ; Rees et Juday, 2002). Il est donc probable que ces types de perturbations affectent différemment les espèces indigènes et exotiques (p. ex. Callaham Jr *et al.*, 2003). Les mécanismes impliqués dans le succès d'envahissement d'*Arion* dans les forêts exploitées pourraient donc différer de ceux favorisant leur envahissement dans les peuplements perturbés par des feux. Afin d'évaluer davantage le rôle des perturbations naturelles dans les invasions biologiques animales, il serait pertinent de tester cette hypothèse dans le cas d'invasion par *Arion* mais également chez d'autres espèces.

4.4 Limites de la thèse

Dans cette thèse, l'évaluation de l'abondance des espèces de limaces a été réalisée à l'aide de plusieurs méthodes : l'utilisation de pièges fosses (chapitre I), de pièges refuges et de la recherche active (chapitre II). Les données des pièges fosses suggèrent que les espèces indigènes sont relativement peu présentes dans les sites de Kenauk et Gagnon (20 fois moins abondantes qu'*Arion* car elle représentait seulement 0.5% des individus collectés dans chacun de ces sites, chapitre I). À l'inverse, l'utilisation de pièges refuges et recherche active dans ces mêmes sites suggèrent que *Philomycus* n'est que sept fois moins abondante qu'*Arion* (chapitre II). Ces résultats sont cohérents avec de précédentes études ayant démontré que selon l'espèce étudiée certaines méthodes sont plus adaptées que d'autres pour les capturer (Archard *et al.*, 2004 ; Cordoba *et al.*, 2011 ; Raudenbush *et al.*, 2021). Dans le cas de cette étude, le biais des pièges fosses en faveur d'*Arion* par rapport à *Philomycus* pourrait provenir des différences de patron spatial d'activé locomotrice entre les deux espèces. En effet, *Arion* semble être très active à la surface de la litière tandis que *Philomycus* utiliserait principalement les débris ligneux au sol pour se déplacer (observation personnelle). Étant donné ces différences de comportement, il est plus probable qu'*Arion* rencontre et tombe dans un piège fosse que *Philomycus*. Ces biais spécifiques aux méthodes d'échantillonnage n'entachent toutefois pas la solidité de nos résultats. En effet, nous n'avons jamais eu pour objectif de comparer l'abondance d'*Arion* à celle de *Philomycus* et toute comparaison d'abondance pour une même espèce entre les différents types de peuplements a été effectuées à l'aide de données récoltés avec la même méthode. Il est toutefois fortement probable que l'abondance des espèces se déplaçant principalement sur la litière, tel qu'd'*Arion*, dans les peuplements forestiers ait été sous-estimée. En effet, la collecte d'échantillon de sol suivi par leur lente immersion permet souvent de collecter plus de limaces que les pièges refuges ou la recherche active (Archard *et al.*, 2004 ; South, 1964 mais voir Cordoba *et al.*, 2000).

L'étude des mécanismes favorisant le succès d'envahissement d'*Arion* à Kenauk suggère que celui-ci aurait été favorisé indirectement par des modifications d'attributs de l'habitat générées par la coupe, entrainant le déclin de *Philomycus* (chapitre II). Il est toutefois possible que la coupe ait affecté un attribut de l'habitat non mesuré dans le cadre de cette étude, et qui aurait directement favorisé le succès d'envahissement d'*Arion* (p. ex. abondance de champignons). À Kenauk, les modifications d'attributs de l'habitat générées par la coupe auraient ainsi pu favoriser directement et indirectement le succès d'envahissement d'*Arion* (hypothèse 3 supportée : Table 2.1a, Figure 2.1c). Cette incertitude n'affecte toutefois pas nos conclusions selon lesquelles

les mécanismes favorisant le succès d'envahissement des espèces exotiques animales peuvent différer à une échelle spatiale fine.

Concernant l'étude des comportements et de leur plasticité en réponse à une variation des conditions d'humidité du sol (chapitre III), nos résultats suggèrent que le comportement d'alimentation et d'utilisation de refuge d'*Arion* pourrait jouer un rôle dans son succès d'envahissement. Nous avions initialement pour objectif d'étudier les conséquences de ces comportements sur l'aptitude phénotypique d'*Arion*, par exemple en mesurant le nombre d'œufs pondus, le nombre d'œufs éclos etc. Malheureusement, cette étude n'a pu être réalisée à cause de de la difficulté de maintenir en captivité *Arion* sur le long terme. L'étude des conséquences de ces comportements sur l'aptitude phénotypique d'*Arion* devra toutefois être réalisée afin de déterminer si le comportement d'*Arion* lui confère un avantage comparativement à *Philomycus* et ainsi, valider que l'hypothèse de l'envahisseur idéal s'applique bel et bien à *Arion*. De plus, l'aspect des coûts reliés à la plasticité, bien qu'ils existent (Callahan *et al.*, 2008), n'a pas été examiné dans la présente étude. Ces coûts (p. ex. ceux liés aux mécanismes sensoriels permettant la plasticité) peuvent varier en fonction des traits, des organismes et des conditions environnementales (Hendry, 2016) et peuvent contraindre l'évolution de la plasticité (p.ex., réduction du degré de plasticité) (DeWitt, 1998). Ainsi, exprimer une importante plasticité en réponse à des variations d'humidités du sol serait moins nécessaire (et potentiellement plus coûteux) chez des individus évoluant dans des habitats peu fréquemment exposés à des stress hydriques que chez ceux évoluant dans des habitats fréquemment exposés à des stress hydriques. Les individus collectés pour l'étude de la plasticité l'ont été dans des forêts matures (potentiellement moins exposées à des stress hydriques). Il est possible que ces individus expriment une plasticité plus faible en réponse à des variations d'humidité du sol que des individus provenant d'habitats perturbés par des coupes forestières (potentiellement plus exposés à des stress hydriques). Comparer la plasticité d'*Arion* en réponse à une variation des conditions d'humidité du sol dans les peuplements matures (i.e., plasticité mesurée dans le cadre de cette thèse) à celle observée dans les habitats perturbés par des coupes forestières serait donc nécessaire afin de déterminer plus précisément si la plasticité peut avoir favorisé le succès d'envahissement d'*Arion*.

Les résultats de nos expériences en milieu contrôlé n'apportent pas la preuve d'une compétition par interférence entre *Arion* et *Philomycus* (chapitre III). Il est toutefois important de rappeler que nous avons commencé à caractériser les comportements des deux limaces présentes dans chaque arène après une période d'acclimatation de 24h. Certaines études démontrent que les individus sont plus agressifs l'un envers l'autre quand ils ne se connaissent pas (p. ex. Puppe, 1998). Afin de déterminer plus précisément si la présence d'*Arion* peut affecter le comportement de *Philomycus*, il serait important de reproduire ces expériences en étudiant les comportements des limaces dès leur installation dans les arènes.

4.5 Perspectives de recherches

Les invasions biologiques dépendent essentiellement de la pression de propagule (le nombre d'individus qui sont introduits et la fréquence de ces introductions ; Lockwood *et al.*, 2005), des caractéristiques de l'écosystème récipiendaire et des caractéristiques de l'espèce exotique (Catford *et al.*, 2009). Dans le cadre de cette thèse, les hypothèses que j'ai testées se rapportaient aux caractéristiques de l'écosystème (attributs de l'habitat et compétition) et à celles de l'espèce exotique (hypothèses de la plasticité et de l'envahisseur idéal). La pression de propagule est un mécanisme clé dans les invasions biologiques au début du processus d'envahissement (c.-à-d., introduction; Dietz et Edwards, 2006 ; Theoharides et Dukes, 2007). L'établissement et l'augmentation de l'abondance de l'envahisseur dans le nouvel environnement dépendront majoritairement des conditions biotiques et abiotiques (Blackburn *et al.*, 2011 ; Theoharides et Dukes, 2007). Les données actuelles supportent l'idée qu'*Arion* est bien établie au Québec (L'Heureux et Angers, 2018 ; Mazaleyrat *et al.*, *submitted*) et que cette espèce est probablement à un stade avancé du processus d’envahissement au Québec, c.-à-d. à la phase d’expansion. Il semble alors plus pertinent de se concentrer sur les caractéristiques de l’écosystème et les caractéristiques d’*Arion* pouvant accroître son succès d’envahissement (c.-à-d. abondance et masse corporelle) que sur le rôle de la pression de propagule dans l’envahissement d’*Arion* dans les habitats perturbés.

Parmi les caractéristiques de l’écosystème qui peuvent favoriser les invasions, le rôle des communautés locales de prédateurs a été peu étudié dans un contexte de perturbation de l’habitat (mais voir : Byers, 2002). La prédation est pourtant un facteur important dans la régulation de la dynamique des populations, et certaines espèces exotiques deviennent envahissantes lorsqu'elles sont exemptes des prédateurs (ou parasites), comme suggéré par l’hypothèse enemy release (Colautti *et al.*, 2004 ; Heger et Jeschke, 2018). Il serait donc intéressant d’identifier les prédateurs des limaces dans nos écosystèmes forestiers et déterminer leur rôle dans le succès d’envahissement des espèces exotiques animales dans les habitats perturbés. Par exemple, les limaces exotiques sont-elles moins prélevées par les prédateurs dans les habitats perturbés que dans les témoins ? Sont-elles moins prélevées par les prédateurs que les espèces indigènes ? Répondre à ces questions, permettrait de mieux comprendre le rôle des facteurs biotiques dans le succès d’envahissement d’*Arion*.

En ce qui concerne les caractéristiques de l’espèce exotique, une attention particulière devrait être portée sur des traits reliés à la reproduction. De précédentes études ont démontré que les espèces exotiques ont généralement une fécondité plus élevée, une plus courte durée de reproduction et une maturité plus précoce que les espèces indigènes (Grabowski *et al.*, 2007 ; Poidatz *et al.*, 2018 ; Vila-Gispert *et al.*, 2005). Préalablement à la mise en place des expériences en milieu contrôlé, j’ai établi un élevage de limace (*Arion* et *Philomycus*) dans le cadre duquel j’ai pu observer des différences marquées dans les stratégies de reproduction de ces espèces. Ainsi, *Arion* allouait son énergie à la production de nombreux mais petits œufs (et elle mourrait après la ponte), tandis que *Philomycus* pondait moins d'œufs mais de taille plus importante (et ne mourrait pas après la ponte), probablement pour augmenter la survie des juvéniles. Le rôle de ces différences de stratégie de reproduction doit être examiné afin de clarifier son rôle dans le succès d'envahissement d'*Arion*, notamment dans les habitats perturbés, et de manière générale, si des stratégies de reproduction sont plus fréquentes chez les espèces animales exotiques envahissantes que chez les espèces indigènes (voir Rambuda et Johnson, 2004 pour les plantes).

Les mécanismes favorisant l'envahissement d'une espèce exotique peuvent varier au cours du temps et des étapes de l'envahissement (Dawson *et al.*, 2009 ; Dietz et Edwards, 2006 ; Gill *et al.*, 2018 ; Theoharides et Dukes, 2007). Malheureusement, les études portant sur l'effet des perturbations sur le succès d'envahissement des espèces exotiques et les mécanismes impliqués sont souvent des études à court terme et sont souvent réalisées peu de temps après l'occurrence de la perturbation (< 5 ans, Jauni *et al.*, 2015). Cette approche ne permet pas d'avoir un portrait global des mécanismes régissant les invasions biologiques et de la dynamique temporelle des invasions. En effet, les invasions biologiques peuvent impliquer de longues périodes d'inactivités relatives suivies de changement apparemment soudain dans la dynamique de l'espèce exotique (Crooks, 2005). La méta-analyse de Jauni *et al.* (2015) démontre que la réponse des espèces exotiques à la perturbation était la plus forte dans les études évaluant leur abondance plusieurs années après la perturbation (> 5 ans). Des études récurrentes dans le même écosystème envahi seraient donc souhaitables tout en offrant la possibilité de caractériser les impacts des espèces exotiques sur une échelle de temps plus longue (Strayer *et al.*, 2006).

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