

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LE NERPRUN BOURDAINE (FRANGULA ALNUS MILLER) : DES IMPACTS MODÉRÉS SUR LA
DIVERSITÉ FLORISTIQUE INDIGÈNE ET DES MACRO-ARTHROPODES SAPROPHAGES

MÉMOIRE PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAITRISE EN SCIENCES DE L'ENVIRONNEMENT

PAR
GABRIELLE ROBERGE

JANVIER 2023

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
Service des bibliothèques

Avertissement

La diffusion de ce mémoire se fait dans le respect des droits de son auteur, qui a signé le formulaire *Autorisation de reproduire et de diffuser un travail de recherche de cycles supérieurs* (SDU-522 – Rév.04-2020). Cette autorisation stipule que «conformément à l'article 11 du Règlement no 8 des études de cycles supérieurs, [l'auteur] concède à l'Université du Québec à Montréal une licence non exclusive d'utilisation et de publication de la totalité ou d'une partie importante de [son] travail de recherche pour des fins pédagogiques et non commerciales. Plus précisément, [l'auteur] autorise l'Université du Québec à Montréal à reproduire, diffuser, prêter, distribuer ou vendre des copies de [son] travail de recherche à des fins non commerciales sur quelque support que ce soit, y compris l'Internet. Cette licence et cette autorisation n'entraînent pas une renonciation de [la] part [de l'auteur] à [ses] droits moraux ni à [ses] droits de propriété intellectuelle. Sauf entente contraire, [l'auteur] conserve la liberté de diffuser et de commercialiser ou non ce travail dont [il] possède un exemplaire.»

REMERCIEMENTS

Tout au long de mon parcours, j'ai eu le privilège de côtoyer de nombreuses personnes incroyables qui ont participé au développement de mon projet. Premièrement, j'aimerais remercier du fond du cœur mon directeur Daniel Kneeshaw et ma co-directrice Tanya Handa. Vous avez rendu possible la réalisation de ce projet d'envergure et vous avez considérablement participé à mon apprentissage en écologie et permis une grande évolution de ma propre personne. Tout ça dans des contextes imprévisibles et chaotiques causés par la Covid-19 !

J'aimerais remercier mes collègues des laboratoires Kneeshaw et Handa, qui ont toutes et tous partagé leurs connaissances avec moi, me permettant d'avancer dans ma recherche. Mention spéciale à Laura-Jeanne Raymond-Léonard, Roberto Sepulveda-Mina, David Grenier Héon, Florentin Jaeger, Marylou Meyer, César Gabillot et Pierce McNie. J'aimerais également remercier mes aides de terrain, Jérémie Campeau-Poirier et Laurie Auclair, sans qui la récolte de données n'aurait jamais été aussi plaisante. Un grand merci également à Pierre-Marc Brousseau, qui a participé à l'identification de mes spécimens d'arthropodes et à Pierre-Olivier Montiglio pour ses précieux conseils en analyses statistiques.

Je veux aussi remercier les membres et mes collègues de l'ISE, du département des Sciences biologiques de l'UQAM, de la Fiducie de conservation des écosystèmes de Lanaudière, de l'organisme CANOPÉE ainsi que le programme MITACS, grâce à qui l'élaboration de mon projet a été possible.

J'aimerais finalement remercier ma famille, amis-es et amoureux-ses de m'avoir supporté et accompagné durant mon parcours académique à la maîtrise, sans qui je n'aurais définitivement pas réussi. J'aimerais souligner la grande implication de mon ami Tristan Juette, qui m'a accompagné considérablement tout le long de l'élaboration de mon mémoire et qui a pris beaucoup de son temps personnel pour m'aider dans l'intégralité de mon projet, en plus de me permettre d'affronter mon syndrome d'imposteur et mes insécurités profondes.

TABLE DES MATIÈRES

REMERCIEMENTS	iii
LISTE DES FIGURES.....	vi
LISTE DES TABLEAUX	viii
RÉSUMÉ	ix
ABSTRACT	x
CHAPITRE 1 INTRODUCTION	1
1.1 Mise en contexte.....	1
1.2 Le nerprun bourdaine (<i>Frangula alnus</i> Miller) – l’espèce cible	4
1.3 But et objectifs de la recherche	7
CHAPITRE 2 INVASIVE GLOSSY BUCKTHORN (<i>FRANGULA ALNUS</i>) A WEAK IMPACT ON PLANTS AND SAPROPHAGOUS MACROARTHROPODS	8
2.1 INTRODUCTION	9
2.1.1 Exotic invasive plant species.....	9
2.1.2 Our target species: <i>Frangula alnus</i> Miller.....	10
2.1.3 Our Study	12
2.2 METHODOLOGY	12
2.2.1 Study site.....	12
2.2.2 Understory plant characterization.....	14
2.2.3 Saprophagous macroarthropod sampling	15
2.2.4 Environmental characterization and measurements	15
2.2.5 Statistical analysis	16
2.3 RESULTS.....	18
2.3.1 Native understory plants	18
2.3.2 Native understory plant communities	20
2.3.3 Native understory plant diversity	21
2.3.4 Saprophagous macroarthropods	23
2.3.5 Saprophagous macroarthropod community composition	24
2.3.6 Saprophagous macroarthropod diversity	25
2.4 DISCUSSION.....	27
2.4.1 Understory native plant species	27
2.4.2 Saprophagous macroarthropods	28
2.4.3 Our system	30
2.4.4 Challenges and limits	30
2.5 APPENDIX.....	32
1.1.1 Horizontal cuts of biggest <i>F. alnus</i> specimens found on site in 2019	32

1.1.2	References for table 2.2 and 2.4.....	33
1.1.3	Summary statistics of RDA of understory plants	34
1.1.4	Polynomial regression of exotic Diplopoda across the gradient of <i>F. alnus</i>	34
1.1.5	Polynomial regression of native Diplopoda across gradient of <i>F. alnus</i>	35
1.1.6	Summary statistics of RDA of macroarthropod communities	36
1.1.7	Diversity indices using litter composition as a predictive variable.....	36
1.1.8	Linear regression model excluding <i>T. rathkii</i>	37
1.1.9	Linear regression model of <i>T. rathkii</i>	38
1.1.10	Other tested environmental explanatory variables.....	39
CHAPITRE 3 DISCUSSION GÉNÉRALE		40
3.1	RETOUR SUR LES POINTS SAILLANTS	40
3.2	CONTROVERSES AVEC <i>FRANGULA ALNUS</i>	41
3.3	CONTROVERSES GÉNÉRALES AVEC LES EVEE.....	42
3.4	GESTION ET INTERVENTION – LES IMPLICATIONS	43
CONCLUSION		45
ANNEXE A. RÉFÉRENCES DE LITTÉRATURE GRISE ET SCIENTIFIQUE SUR L’IMPACT DE <i>F. ALNUS</i> SUR LA DIVERSITÉ DES VÉGÉTAUX.....		46
ANNEXE B. TABLEAU COMPARATIF DE <i>F. ALNUS</i> ET <i>R. CATHARTICA</i> DANS LEURS IMPACTS SUR LES VÉGÉTAUX		48
ANNEXE C. RÉFLEXIONS SUPPLÉMENTAIRES SUR LES INCOHÉRENCES.....		49
BIBLIOGRAPHIE.....		50

LISTE DES FIGURES

Figure 1.1 Fruits et feuilles de *Frangula alnus* (à gauche) et plan rapproché d'une feuille (à droite).
Source: Gabrielle Roberge

Figure 1.2 Carte de la répartition de *Frangula alnus* Miller dans la région des Grands Lacs et dans l'est du Canada et des États-Unis. Sources : INaturalist (2022) et GoogleMap (2022).

Figure 1.3 Zones fortement envahies par *Frangula alnus* au site d'étude. Source: Gabrielle Roberge

Figure 2.1 Location of study site, in L'Assomption, southern Québec. Source: Gabrielle Roberge

Figure 1.2 Map of the location of all 43 sampling plots on study site. Each plot is associated with a density of *Frangula alnus* (individuals 400 m⁻²). All colors on plots are associated with a density interval to facilitate visualisation. The hatched area represents a peatland zone where no plots were installed because woodland-like environmental characteristics were prioritized. Source: Gabrielle Roberge and GoogleMap (2022).

Figure 1.3 Redundancy analysis (see statistical output in Appendix 1.1.3) of all native understory plant species (<1 m in height) according to each sampling plot. Density of *F. alnus* is represented by a gray gradient to visualize the degree of invasion, whereby pale plots have a lower density (0 individual m⁻²) and gradually increase to dark for high density plots (>4 individual m⁻²). Plant species, in red, have been centered and transformed (Hellinger). Constraint variables (canopy cover, average humidity, average pH, and adult density of *F. alnus*), in blue, have also been standardized, centered on 0.

Figure 1.4 Simple linear relationships between the (a) total native understory plant cover (square-root), (b) effective number of native plant species, (c) Shannon-Wiener index, (d) Pielou's evenness index as dependent variables, and density gradient of *F. alnus* (individual m⁻²) as an explanatory variable on the study site.

Figure 1.5 Redundancy analysis (see statistical output in Appendix 1.1.4) of saprophagous macroarthropod communities across sampling plots. Density of *F. alnus* is represented by a gray gradient to visualize the degree of invasion, whereby pale dots have a lower density (0 individual m⁻²) and gradually increase to darker dots for high density plots (> 4 individual m⁻²). The species, in red, have been transformed (log) to minimize the effect of very abundant species and the horseshoe effect. Constraint variables (soil humidity (%), woody debris cover (%), plant diversity (effective number of

native plant species), and native understory plant cover (%)), in blue, were standardized, centered on 0, and vectors were scaled (*1.2) for better visualization.

Figure 1.6 Simple linear relationships between the (a) the effective number species, (b) Shannon-Wiener index, (c) evenness index as dependent variables of saprophagous macroarthropods, and density of *F. alnus* (individual m⁻²) as an explanatory variable on the study site.

Figure 1.2 Feuilles et floraisons de *Frangula alnus* (image du haut), l'espèce étudiée dans le cadre de ce projet. Feuilles et floraisons de *Rhamnus cathartica* (image du bas), l'espèce végétale exotique envahissante souvent associée avec *F. alnus*. Source: Gabrielle Roberge

LISTE DES TABLEAUX

- Table 2.1 Linear regression model outputs of the environmental variables associated with density gradient of *F. alnus* to assess an overview of the environmental conditions across our study site. Some variables that are most likely to influence the density of *F. alnus* were used as independent variables, such as tree canopy cover (%) and pH. Other variables that might be influenced by *F. alnus*, such as soil humidity (%), leaf litter biomass (g m^{-2}), ground-level temperature ($^{\circ}\text{C}$), and woody debris cover (%) were used as dependent variables to determine if they varied across the gradient of *F. alnus*. 17
- Table 2.2 Dominant understory plant species: trees, shrubs, and herbaceous plants (>5 % presence in plots and >5 % vegetation cover) in all 43 plots on our site. Data were collected in 4 circular plots of 1 m^2 (averaged over 1 m^2) for all 43 sampling plots. Shade tolerance, frequency (percentage of presence in plot) and average cover (percentage) of total vegetation for each of dominant understory plant species. 18
- Table 2.3 Linear regressions of density of *F. alnus* (individual m^{-2}) as predictive variables on five diversity index of understory native plant species (height < 1 m). Evenness index and total abundance have been transformed (square roots) to fit linear model conditions. All plant diversity indices are based on the ratio of cover average (to the closest 5%, on 1 m^2) of each species on total plant cover..... 21
- Table 2.4 Abundance, age (juvenile or adult), habitat, and origin (native/exotic) for each species of saprophagous macroarthropods captured in the 43 pitfall traps during the summer of 2020 on the site. 23
- Table 2.5 Descriptive statistics and linear regression outputs of density of *F. alnus* (individual m^{-2}) as predictive variables on five community indices (species richness, effective number of species, Shannon-Wiener index, and evenness index) for saprophagous macroarthropod species. Abundance of millipedes and woodlice have been transformed (square-root) to fit linear model conditions. All arthropod data are based on the average of total abundance of three collects within summer of 2020. 25

RÉSUMÉ

Les espèces exotiques envahissantes (EEE) font partie des acteurs les plus importants associés au déclin de la biodiversité et du fonctionnement des écosystèmes. En accaparant l'espace et les ressources, elles menacent la diversité et la composition des végétaux indigènes, se répercutant ainsi sur les organismes des autres niveaux trophiques. Le nerprun bourdaine (*Frangula alnus* Miller) est une espèce végétale exotique envahissante (EVEE) introduite dans l'est de l'Amérique du Nord vers la fin du 18^e siècle et son expansion est inquiétante pour la biodiversité indigène. Toutefois, contrairement à d'autres EVEE, il y a peu de littérature scientifique sur ses impacts et celle-ci demeure équivoque. Ce projet de recherche avait donc pour but de déterminer si l'augmentation de la densité de *F. alnus* menaçait la diversité et la structure des communautés des plantes indigènes du sous-bois et des macro-arthropodes saprophages (mille-pattes et cloportes). Au cours de l'été 2020, nous avons échantillonné 43 parcelles suivant un gradient de densité de *F. alnus* dans une réserve naturelle envahie, à L'Assomption, au Québec. La couverture des espèces végétales de sous-bois y a été estimée et les macro-arthropodes saprophages ont été capturés avec des pièges-fosses sur deux périodes de 15 jours et une de 14 jours, totalisant 44 jours. Nos principaux résultats ont montré que *F. alnus* n'était pas un acteur fort dans le changement en composition des espèces dans les communautés des deux groupes étudiés. Toutefois, pour les plantes des sous-bois, on remarque une diminution du nombre effectif d'espèces, de l'indice de Shannon-Wiener et de l'indice de Pielou, suggérant une tendance à l'homogénéisation des espèces lorsque la densité de *F. alnus* augmente. Les macro-arthropodes saprophages ont également montré une légère diminution de ces mêmes indices et de la richesse spécifique en fonction de *F. alnus*, principalement causée par l'espèce exotique *T. rathkii* (Oniscidae). Les effets observés sont moins prononcés qu'attendu et soulèvent que *F. alnus* serait une espèce moins compétitive en comparaison à d'autres (e.g., *R. cathartica* ou *F. japonica*) pour la diversité des plantes indigènes et des macroarthropodes saprophages. Ces résultats soulèvent des nuances dans la perception de la sévérité des impacts de *F. alnus* sur la biodiversité des milieux qu'il envahit. Nos observations sont donc congruentes avec l'ambiguïté dans la littérature, soulignant des nuances quant aux impacts de *F. alnus* sur la diversité. Cela soulève également des discussions sur les complications générales retrouvées dans l'évaluation des impacts de *F. alnus* et des autres EVEE. Nous proposons donc des solutions aux problématiques associées à l'évaluation de leurs impacts sur la biodiversité et leur gestion.

Mots clés : invasion, plante exotique envahissante, Effet bottom-up, écologie des communautés, Diplopodes, Isopodes, Oniscidea, mille-pattes, cloportes

ABSTRACT

Invasive alien species (IAS) are among the most important drivers associated with the decline of biodiversity and ecosystem functioning. By monopolizing space and resources, they threaten the diversity and composition of native plants, thus affecting organisms at other trophic levels. Glossy buckthorn (*Frangula alnus* Miller), an invasive alien plant species (IAPS) introduced to eastern North America at the end of the 18th century, is expanding rapidly and is a potential threat for native biodiversity. However, unlike other IAPS, the scientific literature on the impacts of *F. alnus* is still scarce and equivocal. The purpose of this research project was therefore to determine whether the increase in the density of *F. alnus* altered the structure of the communities and the diversity of both understory native plants and saprophagous macroarthropods (millipedes and terrestrial woodlice). During the summer of 2020, we sampled 43 plots following a density gradient of *F. alnus* at an invaded nature reserve, in L'Assomption, Quebec. The cover of understory plant species was estimated and saprophagous macroarthropods were captured with pitfall traps over two periods of 15 days and one of 14 days, totaling 44 days. Our main results showed that *F. alnus* was not a strong driver in change in species composition for both studied groups. However, for understory plants, we observed a homogenization tendency as the effective number of species, the Shannon-Wiener index, and the evenness index decreased when the density of *F. alnus* increased. Saprophagous macroarthropods also showed a slight decrease in these same indices and in species richness along the gradient of *F. alnus* density, mostly driven by the exotic species *T. rathkii* (Oniscidae). The observed effects are less pronounced than expected and suggest that *F. alnus* would be a less destructive species than other IAPS (i.e., competitive species such as *R. cathartica*, *F. japonica*) on the diversity of native understory plants and saprophagous macroarthropods. Our results are congruous with the inconsistencies observed in the literature, suggesting recurring issues in the assessments of the impacts of *F. alnus* and other IAPS. We thus suggest several solutions to improve future scientific research and IAPS management.

Keywords: Invasion, alien invasive plant, community ecology, bottom-up effect, Diplopoda, Isopoda, Oniscidea, millipede, woodlice

CHAPITRE 1

INTRODUCTION

1.1 Mise en contexte

Il n'y a plus de doute aujourd'hui sur le fait que les systèmes biologiques à l'échelle globale sont gravement affectés par l'activité humaine; un huitième des espèces font face à l'extinction, les structures biotiques et abiotiques des écosystèmes sont altérées et les services qu'ils procurent diminuent considérablement (IPBES, 2020; IPCC, 2022). Associées avec le réchauffement climatique, la fragmentation de l'habitat et l'utilisation des terres, les espèces exotiques envahissantes (EEE) font partie des enjeux les plus préoccupants pour la biodiversité à l'échelle globale (IPBES, 2020; IPCC, 2022; Shrestha et al., 2018; Vitousek et al., 1996). Malgré les très récentes mesures en place pour leur gestion (autour des 1970 en Amérique du Nord), elles sont reconnues depuis plusieurs centaines comme étant problématiques puisqu'elles ont rarement d'agents de contrôle dans leur nouveau milieu (Simberloff, 2013). Le gouvernement du Canada définit une espèce exotique comme « une plante, un animal ou un microorganisme qui a été introduit, du fait de l'activité humaine, ailleurs que dans son aire passée ou présente de répartition naturelle » (Gouvernement du Canada, 2004). Une espèce exotique obtient donc le statut « envahissant » lorsque sa propagation pose un risque sur le nouvel environnement qu'elle introduit (Gouvernement du Canada, 2004). Simberloff (2013) spécifie également que l'espèce introduite doit se perpétuer et se propager en dehors de son point d'arrivée et se reproduire sans assistance humaine. Aujourd'hui, nous savons qu'elles ont globalement des impacts négatifs importants (dans le sens statistique du terme) sur plusieurs secteurs sociétaux et économiques ainsi que sur l'équilibre biotique et abiotique des écosystèmes (Colautti et al., 2006; GISS, 2005; Lavoie, 2019; Lavoie et al., 2014; NEPA, 1970; Olson, 2006; Simberloff, 2013). Leur forte compétitivité peut diminuer la diversité génétique et spécifique des espèces indigènes ainsi que modifier la composition des communautés à travers les niveaux trophiques, influençant les processus écosystémiques (Chapin III et al., 2000). Puisque généralement une grande diversité est associée à une meilleure productivité primaire et une plus grande résilience de l'écosystème - en milieu naturel ou agricole - une atteinte à la diversité peut être dramatique pour les fonctions écosystémiques (IPBES, 2019; Sanford et al., 2021; Tilman, 2000).

Les espèces végétales exotiques envahissantes (EVEE) sont définies comme des plantes nuisibles introduites par les humains (volontairement ou accidentellement) à partir d'un autre continent ou d'une région très éloignée et qui colonisent de nouveaux territoires à un rythme rapide, produisant des

populations dominantes (Lavoie, 2019). L'aspect de nuisibilité s'applique également dans la définition et correspond aux plantes nuisant à la biodiversité, au maintien des fonctions écosystémiques, à la santé humaine, à l'agriculture, aux productions horticoles, à la foresterie et à la santé des bestiaux (Lavoie, 2019). Dans le cadre de ce mémoire, l'aspect de nuisibilité sera donc implicite lors de mentions aux espèces exotiques envahissantes.

On estime à ce jour, dans l'est du Canada, qu'entre 25% et 33,5% des espèces végétales sont exotiques et environ 10% d'entre elles seraient des EVEE (Lavoie, 2019). L'augmentation de leur répartition et densité ne montre aucun signe de ralentissement, autant au Canada que partout dans le monde (Kumar Rai & Singh, 2020; Lalk et al., 2021; Lavoie, 2019; Lowry et al., 2013). Elles menacent des milieux économiques importants, tels l'agriculture, la foresterie, le tourisme et y engendrent des coûts très élevés (Anderson, 2012; Colautti et al., 2006; Olson, 2006; Pimentel et al., 2000). À titre d'exemple, les deux espèces végétales exotiques envahissantes *Centaurea maculosa* (centaurée maculée) et *Euphorbia esula* (euphorbe ésole) occasionnent ensemble des coûts évalués à 38,21 millions de dollars par années sur le territoire canadien (Colautti et al., 2006; Olson, 2006). Le rapport *Invasive Alien Plants in Canada* estime également une perte cumulée de 2.2 milliards de dollars associés aux plantes exotiques envahissantes dans le milieu de l'agriculture (Canadian Food Inspection Agency, 2008).

En plus des conséquences anthropocentriques, les EVEE représentent une menace pour l'intégrité des écosystèmes et peuvent provoquer des déséquilibres importants dans les dynamiques des communautés en compétitionnant fortement avec les espèces végétales locales et en monopolisant les niches écologiques (Callaway & Maron, 2006; Lavoie, 2019). La présence importante de certaines EVEE et leurs impacts sur la diversité s'expliquent par leur forte compétitivité et leurs nombreux mécanismes de propagation efficaces (Lavoie, 2019). En plus d'être facilitées par des perturbations anthropiques des milieux (i.e., déboisement à la suite de projets d'aménagement d'infrastructures, fractionnement d'habitat par des routes) et d'avoir peu (ou aucun) de prédateurs naturels, elles possèdent des stratégies de colonisation avantageuses : croissance et propagation rapide, phénologie compétitive et reproduction efficace. Par exemple, plusieurs espèces, telle *Phragmites australis* (roseau commun), *Rhamnus cathartica* (nerprun cathartique) et *Avena fatua* L. (folle avoine), vont faire une quantité spectaculaire de graines pouvant rester dans le sol de nombreuses années et émerger lorsque les conditions sont propices (Lavoie, 2019). De plus, la plupart vont également avoir une multiplication végétative rapide (i.e., fragmentation, bouturage, marcottage, drageons, rhizomes) leur permettant d'augmenter leur recouvrement au détriment des plantes moins compétitrices à proximité. Certaines, telles *Rosa multiflora* (rosier multiflore)

et *Berberis thunbergii* (épine-vinette de Thunberg) ont des feuillages très denses qui limitent grandement l'accès de la lumière aux plantes basses, limitant ainsi leur croissance (Yates et al., 2004). D'autres, comme *Centaurea diffusa* (centaurée diffuse), *Rhamnus cathartica* (nerprun cathartique) ou *Ailanthus altissima* (ailante glanduleux), contiennent des substances herbicides (allélopathiques), pouvant potentiellement inhiber la survie des végétaux à proximité (Callaway & Ridenour, 2004; Pisula & Meiners, 2010; Vivanco et al., 2004; Warren et al., 2017). Les EVEC sont également connues pour modifier les composantes chimiques, le microbiote et les cycles de décomposition des sols et de la litière de feuilles (Callaway & Ridenour, 2004; Ehrenfeld, 2003; Heneghan et al., 2002; McLeod et al., 2016). En plus de tous ces mécanismes, certaines vont également faire de la co-facilitation avec d'autres EVEC (e.g., *R. cathartica* avec le ver de terre européen et l'étourneau sansonnet), amplifiant ainsi leur mutuelle capacité d'invasion (Heimpel et al., 2010; Roth et al., 2015). Ces différents mécanismes permettent aux EVEC d'altérer la structure des milieux qu'elles envahissent, modifiant ainsi la disponibilité des niches pour les espèces végétales indigènes. Dans certains milieux, on observe même des espaces de monoculture de certaines EVEC. Les autres espèces voient donc leur diversité spécifique, abondance et succès reproductif fortement réduits face à cette compétition agressive (Callaway & Ridenour, 2004; Molano-Flores, 2014).

Une perturbation des producteurs primaires peut ensuite se propager dans les autres niveaux trophiques, affectant donc l'écosystème dans son ensemble (Brousseau et al., 2021; Gerber et al., 2008; Heimpel et al., 2010). Comme stipule l'hypothèse de la spécialisation de la ressource (Southwood et al. 1979), souligné par Brousseau et al. (2021), une grande diversité dans les ressources serait congruente avec une grande diversité dans les consommateurs. L'invasion par une EVEC menace donc une grande variété d'organismes au sein d'un écosystème. Parmi ceux-ci, les détritivores saprophages, consommateurs de matière ligneuse, sont un groupe important dans les processus écosystémiques en participant activement du cycle de carbone et d'azote (Cárcamo et al., 2000). À travers leur étude sur un gradient latitudinal, Handa et ses collègues (2014) ont d'ailleurs soulevé un effet important de la diversité fonctionnelle des autotrophes en lien avec la diversité des décomposeurs et leur rôle sur les cycle du carbone et de l'azote, soulignant ainsi leur importance. De plus, certains macro-arthropodes saprophages, comme les mille-pattes (Diplopoda) et les cloportes (Isopoda) sont reconnus comme sensibles aux perturbations (Paoletti & Hassall, 1999; Wenk et al., 2016)

1.2 Le nerprun bourdaine (*Frangula alnus* Miller) – l'espèce cible



Figure 1.1 Fruits et feuilles de *Frangula alnus* (à gauche) et plan rapproché d'une feuille (à droite). Source : Gabrielle Roberge

Le nerprun bourdaine (*Frangula alnus* Miller) est un arbuste de la famille des Rhamnacées (Figure 1.1) introduit à la fin des années 1800 envahissant et problématique dans l'est de l'Amérique du Nord (Aiello-Lammens, 2020; Catling & Porebski, 1994; Lavoie, 2019). Il est originaire d'Asie et d'Europe et a été importé pour ses propriétés médicinales et ornementales. Sa répartition augmente à un risque alarmant dans l'est de l'Amérique du Nord depuis la fin des années 1900; avec une proportion d'observations doublée entre 1950 et 1990 (Aiello-Lammens, 2020; De Kort et al., 2016; Frappier et al., 2003; Lavoie, 2019). Il est retrouvé aujourd'hui principalement dans les régions maritimes ainsi que dans les provinces et États de l'est, allant du sud des Grands Lacs jusqu'au Manitoba et la Saskatchewan (Figure 1.2). Les impacts de *Frangula alnus* sur la biodiversité ont été mentionnés à plusieurs reprises par une grande variété d'agences à travers des documents scientifiques, gouvernementaux, littérature grise ainsi que de nombreux témoignages (Anderson, 2012; Hébert & Thiffault, 2014; Higman, 2009; Martel, 2021; Michigan Department of Natural Resources, 2012; Schoeb et al., 2012). En effet, les caractéristiques physiologiques du nerprun bourdaine lui permettent une grande efficacité dans la colonisation de certains milieux. Le débourrement précoce de ses bourgeons et la grande densité de son feuillage peuvent nuire aux espèces végétales de la strate herbacée (Converse, 1984; Godwin, 1943). De plus, sa résistance aux sols plus acides et humides lui permet d'aisément envahir les tourbières et milieux humides (Lavoie, 2019).

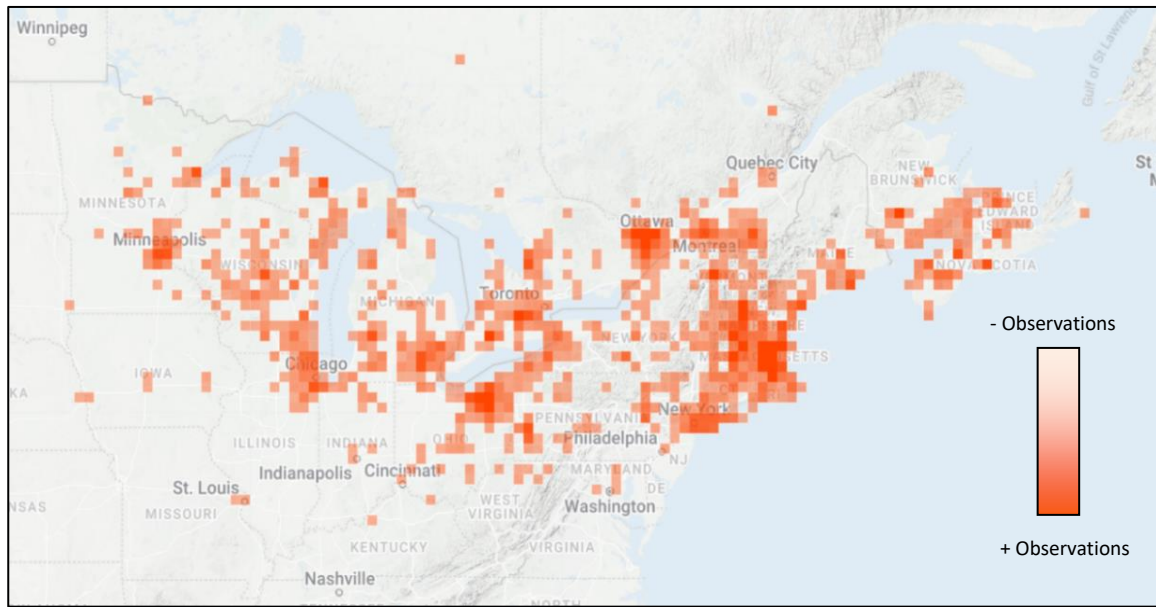


Figure 1.2 Carte de la répartition de *Frangula alnus* Miller dans la région des Grands Lacs et dans l'est du Canada et des États-Unis. Sources : INaturalist (2022) et GoogleMap (2022).

Mais les études scientifiques de l'impact de *F. alnus* sur la diversité floristique et faunique soulèvent des résultats ambivalents. Parmi celles répertoriées lors de ce projet, certaines ne montrent aucun effet de *F. alnus* sur les plantes herbacées (Mills et al., 2009) et d'autres, rapportent une inhibition significative de l'établissement des semis d'arbres, mais aucune sur les plantes herbacées (Frappier et al., 2004). Houlihan et Findlay (2004) et Possesski *et al.* (2000) ont même rapporté une hausse de diversité, chez certains arbustes et végétaux indigènes. Néanmoins, quelques études rapportent des relations négatives de *F. alnus* sur certains groupes de plantes, telles qu'une diminution de la densité des semis d'arbres indigènes, du couvert et de la richesse spécifique des plantes herbacées et un changement des structures communautaires en faveur des espèces tolérantes à l'ombre (Fagan & Peart, 2004; Frappier et al., 2003; Hamelin et al., 2017).



Figure 1.3 Zones fortement envahies par *Frangula alnus* au site d'étude.
Source: Gabrielle Roberge

Par le fait même, deux études moins récentes montrent une capacité de *F. alnus* à coloniser rapidement et dominer dans des milieux humides et tourbières (Reinartz & Kline, 1988; Taft & Solecki, 1990). Reinartz et Kline (1988) ont d'ailleurs observé que *F. alnus* peut entraîner des conséquences catastrophiques sur le milieu humide, avec une population augmentant sur une tendance logarithmique. De plus, Stokydyk et Hermann (2014 et 2016) ont souligné que les composantes des feuilles du nerprun bourdaine modifient la dynamique du sol et agissent sur la minéralisation de l'azote total, provoquant des changements dans les mécanismes de décomposition de la litière et les fonctions de la communauté microbienne. Finalement, seulement une étude relie le nerprun bourdaine et la biodiversité des arthropodes ; où l'on observe une augmentation de l'abondance et de la composition des espèces d'insectes pollinisateurs à la suite de l'élimination de *F. alnus* (Fiedler et al., 2012). Malgré l'ambivalence des impacts associés à *F. alnus* dans la littérature scientifique, sa présence importante (Figure 1.3), sa capacité d'envahissement ainsi que les mécanismes de propagations qu'il utilise soulèvent tout de même de grandes inquiétudes. C'est pourquoi il est important d'approfondir les recherches scientifiques sur les risques et impacts que cette espèce représente sur la diversité indigène.

1.3 But et objectifs de la recherche

Le but de ce mémoire consiste à déterminer l'influence de *Frangula alnus* sur la diversité et la composition taxonomiques de deux groupes d'organismes, soit les plantes indigènes de sous-bois et les macroarthropodes saprophages. Sachant que les mécanismes de propagation de *Frangula alnus* comportent des risques réels, similaires à beaucoup d'autres EVEC, les hypothèses émises sont que *F. alnus* (1) modifiera la composition spécifique des communautés et (2) diminuera la diversité taxonomique des plantes de sous-bois. De plus, comme mentionné précédemment, en tant que premiers consommateurs du réseau trophique de matière organique et en fonction de l'hypothèse de spécialisation de la ressource, les communautés des macroarthropodes saprophages sont à risque de subir l'effet *bottom-up* par la perte de diversité des essences végétales et l'augmentation du ratio d'essence de *F. alnus* dans la litière forestière. Il est donc également attendu que ces communautés subissent des effets similaires aux végétaux, soit (3) une altération dans la composition spécifique de leur communauté et (4) une diminution de leur diversité taxonomique.

Cette recherche présentée sous forme d'article scientifique apportera davantage de connaissances sur les effets de *Frangula alnus* sur la biodiversité dans une réserve naturelle fortement envahie à proximité de la région métropolitaine de Montréal. Elle apportera plus de clarté sur l'influence de cette EVEC et permettra de minimiser l'ambivalence observée dans la littérature quant à ses impacts sur la biodiversité. Le chapitre suivant sera soumis pour publication et étudiera la composition et de la diversité des végétaux de sous-bois et des arthropodes saprophages. Au total, pendant l'été 2020, 43 placettes ont été réparties suivant un gradient de densité de *F. alnus*, allant d'aucun individu à une densité élevée (> 4 individus par m²). Pour chacun des groupes, nous avons procédé à un inventaire taxonomique à l'espèce ainsi qu'une récolte de données d'abondance, pour ensuite calculer plusieurs indices de diversité (nombre effectif d'espèces, indice de Shannon-Wiener et de Pielou). Plusieurs autres données environnementales telles que le recouvrement de la canopée par les arbres, le taux d'humidité, pH et température du sol ont également été récoltées. Finalement, trois quadrats de 15 x 15 cm sur chaque placette ont été récoltés afin d'obtenir la biomasse sèche de la litière ainsi que la composition en espèces de celle-ci. Le chapitre 3 est présenté sous forme de discussion générale abordant les problématiques rencontrées dans notre étude. Différentes observations et réflexions en fonction de nos résultats ont été soulevées et mises en relation avec certaines controverses associées à la littérature sur *Frangula alnus* et les EVEC. Ces réflexions soulèvent notamment quelques pistes de solutions pour des études antérieures et de nouvelles perspectives pour l'évaluation et le contrôle des espèces végétales exotiques envahissantes.

CHAPITRE 2

INVASIVE GLOSSY BUCKTHORN (*FRANGULA ALNUS*) A WEAK IMPACT ON PLANTS AND SAPROPHAGOUS MACROARTHROPODS

Abstract

Invasive alien plant species (IAPS) are generally associated with a decline in native plant diversity, thus affecting organisms at other trophic levels. Glossy buckthorn (*Frangula alnus* Miller) is an invasive alien shrub introduced to eastern North America in the late 1800s, but scientific knowledge on its impact on flora and fauna is still ambivalent. We sought to determine whether the density increase of *F. alnus* threatened the diversity and altered the species found in the community of understory native plants and saprophagous macroarthropods (millipedes and woodlice) on a recently invaded nature reserve, in southern Québec, Canada. During summer 2020, we sampled 43 plots following a density gradient of *F. alnus* (height > 1 m), where the cover of understory plant species was estimated and the saprophagous macroarthropods were captured over two 15-days and one 14-days periods using pitfall traps. In total, 20.5% of the understory plant cover was composed of *F. alnus* seedlings and saplings. Adult density did not influence understory plant community structure, but we observed a decline in the effective number of species, Shannon-Weiner, and evenness indices, suggesting a homogenization tendency and dominance by *F. alnus*. For saprophagous macroarthropods, a total of 10 species were observed (i.e., 9 diplopods and only 1 species of isopod). The structure of the communities was mostly influenced by environmental variables such as percentage of woody debris and soil humidity, and barely by *F. alnus*. Saprophagous macroarthropods also showed a slight decrease in these same indices and specific richness along the gradient of *F. alnus* density, mostly driven by the exotic species *T. rathkii* (Oniscidae). These results, in a recently invaded ecosystem, suggest that *F. alnus* might not present the same threat to native biodiversity when compared to other IAPS, like *R. cathartica* and *F. japonica*. Overall, our results were less pronounced than expected and consistent with the ambivalence found in the literature regarding *F. alnus*, implying that it could coexist with species native to our studied system. However, systemic methodological problems when assessing invasive species should also be considered.

2.1 INTRODUCTION

2.1.1 Exotic invasive plant species

In the past few decades, a lot of concerns have been raised by the scientific communities around loss of biodiversity in ecosystems (IPBES, 2019). It can considerably compromise the efficiency in ecosystem functions, such as reducing resilience, stability, and primary productivity (Butenschoen et al., 2014; Cardinale et al., 2012; IPBES, 2019). Invasive alien species (IAS) are a worldwide concern known to be one of the main drivers having negative impacts on biodiversity, ecosystem services, and several societal and economic sectors (IPBES, 2019; Simberloff, 2013; Vitousek et al., 1996). Among others, invasive alien plants species (IAPS) can cause great biological disturbance in the ecosystems they invade through fierce competition with native plants and leading the specific diversity in local ecosystems to decline (Kumar Rai & Singh, 2020; Lalk et al., 2021; Lavoie, 2019; Litt et al., 2014; Lowry et al., 2013). In Canada, roughly 30% of total plant species are estimated to be non-native and around 10% are estimated to be invasive, having negative impacts on biodiversity and high costs in different important economic sectors (Anderson, 2012; Brouillet et al., 2010; IPBES, 2019; Lavoie, 2019; Vyn, 2019).

IAPS are strong competitors to native plant species as they have advantageous reproductive mechanisms, competitive phenology, no natural predators and can alter biotic and abiotic conditions within the system they invade (Gooden & French, 2014; Kumar Rai & Singh, 2020; Lavoie, 2019; Pyšek et al., 2012; Vilà et al., 2011; Vitousek et al., 1996). For example, several species, such as *Rosa multiflora* (Japanese rose) and *Berberis thunbergii* (Japanese Barberry) have very dense thickets and foliage, which greatly limits access to light for lower plants (Yates et al., 2004). A great number of species, such as *Phragmites australis* (common reed), will propagate very rapidly, as they produce a lot of seeds and spread rapidly via vegetative propagation (Lavoie, 2019). Several are also known to be associated with altered soil chemistry, microbiomes, and rapid decomposition processes, inducing changes in the structure of the soil and leaf litter composition and quality (Heneghan et al., 2002; Heneghan et al., 2004; McLeod et al., 2016). Some, like *Ailanthus altissima* (Tree of Heaven), and *Rhamnus cathartica* (Common Buckthorn) even contain allelopathic substances in their tissues, potentially inhibiting the survival of nearby plants (Callaway & Ridenour, 2004; Ehrenfeld, 2003; Pisula & Meiners, 2010; Warren et al., 2017).

These general mechanisms found in IAPS are a great advantage in competition among plants and can negatively impact primary producers by decreasing their diversity, relative abundance and total abundance, thus subsequently disturb the food web, causing loss of diversity and community species

alteration on all trophic levels through the *bottom-up* effect (Burkle et al., 2012; Hejda et al., 2009; McCary et al., 2016; Salamon et al., 2011). This is also a corollary of the *resource specialization hypothesis*, which stipulates that diversity in resources favors diversity in consumers (Southwood et al., 1979). Conversely, a decrease in resources diversity should provoke a decrease in consumers, as we expect a covariability among trophic levels, whether taxonomically or functionally (Brousseau et al., 2019). For example, Schuh and Larsen (2015) documented a decrease in the abundance and diversity of crawling predatory insects, caused by the lack of availability of prey in areas invaded by *R. cathartica*. Brousseau *et al.* (2021) also reported a decrease in the richness and diversity of plant functional traits in plots dominated by the IAPS *Fallopia japonica*. They observed that the presence of this plant strongly reduces correlations between functional traits of prey and predators in edaphic arthropods, suggesting that *F. japonica* disrupts functional linkages in the food web.

Since IAPS can potentially induce diversity loss in primary producers and spread through the trophic network, it is relevant to investigate how IAPS may influence community structure of plants but also organisms that they interact with. A loss of plant diversity due to IAPS could lead to a diversity loss in primary consumers and other trophic levels, in both green (grazing) and brown (detrital) food webs (Siemann, 1998; Southwood et al., 1979). For example, ground-dwelling arthropod abundance, composition, and diversity can be greatly affected by changes in species composition of litter and soil quality due to IAPS (Garcia-Tejero & Taboada, 2016; Gerber et al., 2008; Lalk et al., 2021; Litt et al., 2014). Saprophagous macroarthropods are known to have a great impact on decomposition dynamics in temperate terrestrial ecosystems and contribute significantly to general soil invertebrate diversity (Gerlach et al., 2013; Handa et al., 2014). In general, brown food webs are hypothesized to be more resilient as detritivores tend to have a wide diversity of feeding guilds and no immediate effect on the resource input, thus an effect only through the *bottom-up effect* (Blair et al., 1994; Moore et al., 2004). But in a meta-analysis of 35 papers studying relationships between IAPS and brown food webs, McCary *et al.* (2016) observed that in woodlands, conversely to wetlands and grasslands, detritus eater abundance was negatively impacted by the presence of IAPS.

2.1.2 Our target species: *Frangula alnus* Miller

Our species of interest, Glossy Buckthorn (*Frangula alnus* Miller), is a Rhamnaceae shrub considered to be invasive and problematic in eastern North America and was introduced in the late 1800s (Aiello-Lammens, 2020; Catling & Porebski, 1994; Converse, 1984; Godwin, 1943; Hébert & Thiffault, 2014; Lavoie, 2019). It

is native to Asia and Europe and was imported for its medicinal and ornamental properties (Aiello-Lammens, 2020; De Kort et al., 2016; Delanoy & Archibold, 2007; Frappier et al., 2003; Lavoie, 2019). Distribution of *Frangula alnus* has been increasing at an alarming rate in eastern North America since the mid-1900s with an exponential increase in the number of species records (Aiello-Lammens, 2020; De Kort et al., 2016; Lavoie, 2019). The early burst of its buds, the density of its foliage and dense thickets, as well as the late dropping of leaves in the fall can be harmful to understory plant species (Converse, 1984; Godwin, 1943). To date, peer-reviewed studies on the impact of *F. alnus* on flora diversity raise ambivalent results. Some show no effect on understory plants (Houlahan & Findlay, 2004; Mills et al., 2009) or even an increase in shrub species richness (Possessky et al., 2000). Frappier et al. (2004) observed a significant inhibition of tree seedling establishment (mostly *Acer rubrum*, *Fraxinus americana*, *Pinus strobus*, and *Quercus rubra*), but not of herbaceous plants. Some studies also reported negative relationships in certain groups of plants, such as a decrease in the density of native tree seedlings, herbaceous cover, and specific richness, and changes in community structures in favor of shade-tolerant species (Fagan & Peart, 2004; Frappier et al., 2003). Moreover, Stokdyk and Hermann (2014 & 2016) observed that leaf extracts of *F. alnus* altered soil dynamics and act on total extractable nitrogen (TEN) mineralization, causing changes in litter decomposition mechanisms and microbial community function. Also, we found only one study that assesses the interactions between *F. alnus* and arthropod diversity; where an increase in the abundance and diversity of generalists pollinating insects followed the removal of *F. alnus* (Fiedler et al., 2012). Therefore, no study assessing *F. alnus* with soil arthropods was ever done, even if they are a relevant group to study interactions within ecological processes (Coyle et al., 2017; Wenk et al., 2016).

Among soil edaphic organisms, saprophagous macroarthropods (millipedes and woodlice), are known to be sensitive to disturbance and can be used as bioindicators (Paoletti & Hassall, 1999; Wenk et al., 2016). They are the first line of organic matter shredders in the brown food web and are known for their essential roles in decomposition cycles (David & Handa, 2010; Hopkin & Read, 1992; Langor et al., 2019; Shelley, 1988). Millipedes (Diplopoda) and woodlice (Isopoda) are large terrestrial detritivores (5-50 mm) that are generally less studied than other detritivores and macroarthropod groups when it comes to IAPS invasions. As first line organisms in the brown food web, they facilitate the decomposition process by shredding and digesting plant material, thus facilitating access of nutrients to smaller decomposers and microbiomes (Cárcamo et al., 2000; David & Handa, 2010; Hopkin & Read, 1992; Langor et al., 2019; van Gestel & Loureiro, 2018). They are relevant in assessing impacts of IAPS because they tend to respond negatively to decreased food quality (David & Handa, 2010; De Oliveira et al., 2010). Woodlice are also known to be good bio-indicators of disturbances in ecosystems, especially the specialists, who tend to react negatively

to disturbances (Magura et al., 2008; van Gestel & Loureiro, 2018). Like other ground-dwelling arthropods, their diversity and community structure are likely to suffer from alterations of habitat provoked by an IAPS.

2.1.3 Our Study

Our goal was to study the impact of *F. alnus* on community composition and diversity of understory plants and saprophagous macroarthropods to assess biodiversity risks associated with this IAPS. We tested the influence of *Frangula alnus* through a density gradient on understory plants and saprophagous macroarthropods in an invaded woodland. As *F. alnus* takes over and alters understory plant communities, we should observe similar results with saprophagous macroarthropods, as they live and feed on leaf litter beneath *F. alnus*. We therefore hypothesize that the increase in the density of *F. alnus* will (1) modify the structure of plant species communities in the understory layer and (2) reduce their specific taxonomic diversity. The increasing of *F. alnus* density and its leaf ratio in the litter, as well as the diversity loss of native understory plants species also suggests that (3) the specific composition of the saprophagous macroarthropod communities will be altered, (4) and their specific diversity should decrease.

2.2 METHODOLOGY

2.2.1 Study site

The study site was located in a new natural reserve (Bouchard, 2022), surrounded by agricultural lands in southern Québec, Canada and covered 12 ha of deciduous forest in an area of wetlands, early succession woodlands, and peatlands (Figure 2.1). Little is known about saprophagous macroarthropod communities specific to these ecosystems, but we know that millipedes tend to live in humid environments (Hopkin & Read, 1992) and woodlice can be found around peatlands and wetlands (Brigić et al., 2017). Moreover, these ecosystems are known to support a great diversity and abundance in invertebrates (Batzer & Boix, 2018). Since 2016, a significant increase in *F. alnus* on this site has been documented and a gradual degree of invasion is perceptible in the woodlands, whereby very dense plots visually had > 85 % foliage cover by *F. alnus* (Gabillet et al., 2019). We estimated that the invasion happened about 26 years ago, after the commercial exploitation of peatland soil ended, in 1996 (CPTAQ, 1996). This was confirmed by coring the biggest individuals which were found to be around 27 years old (Dumas, Meyer, personal communication, see Appendix 1.1.1). Woodlands on the site were mainly dominated by pioneer trees, such as *Acer rubrum* (red maple), *Populus tremuloides* (quaking aspen), and *Betula populifolia* (gray birch). Several species of

Rubus and Pteridophytes were also found in great abundance. The presence of peatlands and low pH (average of 4.00 on the study site) show that the soil was very acidic (Pansu & Gautheyrou, 2006).

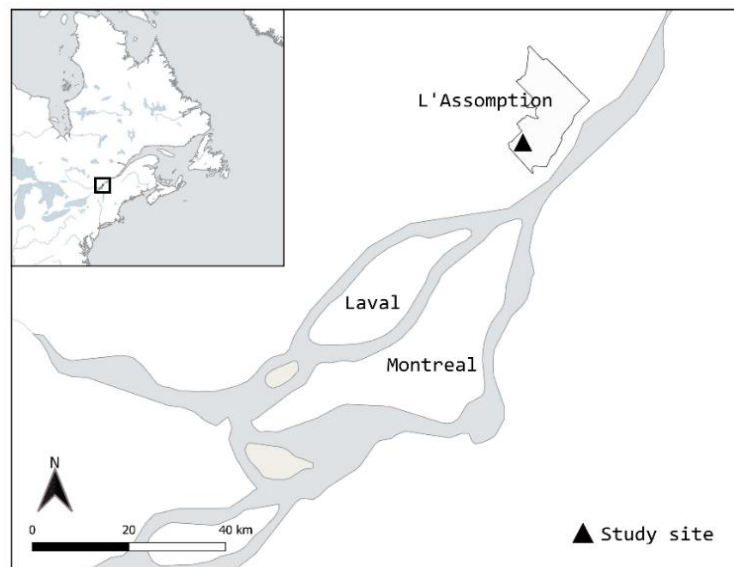


Figure 2.1 Location of study site, in L'Assomption, southern Québec. Source : Gabrielle Roberge

To assess the influence of *F. alnus* on native understory plants and saprophagous macroarthropod communities, 43 sampling plots were placed at a minimum distance of 40 m from each other, following a density gradient of *F. alnus*. The gradient was determined following an exploration of the site and estimation of percentage of cover by *F. alnus* (height > 1 m). We then established plots and counted each individual on 5 m² or 50 m² (depending on the estimated density) and scaled to 400 m² for visualisation of the invasion gradient (Figure 2.2). Density of *F. alnus* was scaled to 1 m² for statistical analysis, giving a range from 0 to > 4 individuals m⁻². The peatland zone (no tree canopy and covered mostly in *Rhododendron canadense* and *Kalmia angustifolia*) was not sampled in order to focus on areas with woodland attributes, ensuring similar biotic structures and soil conditions. Each plot was centered on a pitfall trap and made of several circular plots: four of 1 m², one of 5 m², and one of 50 m². The size of the plots was associated with the size and density categories of *F. alnus* and characterized vegetation type. On the site, with an average of 20.5%, *Frangula alnus* was the species with the largest area of total cover on ground level (Table 2.2).

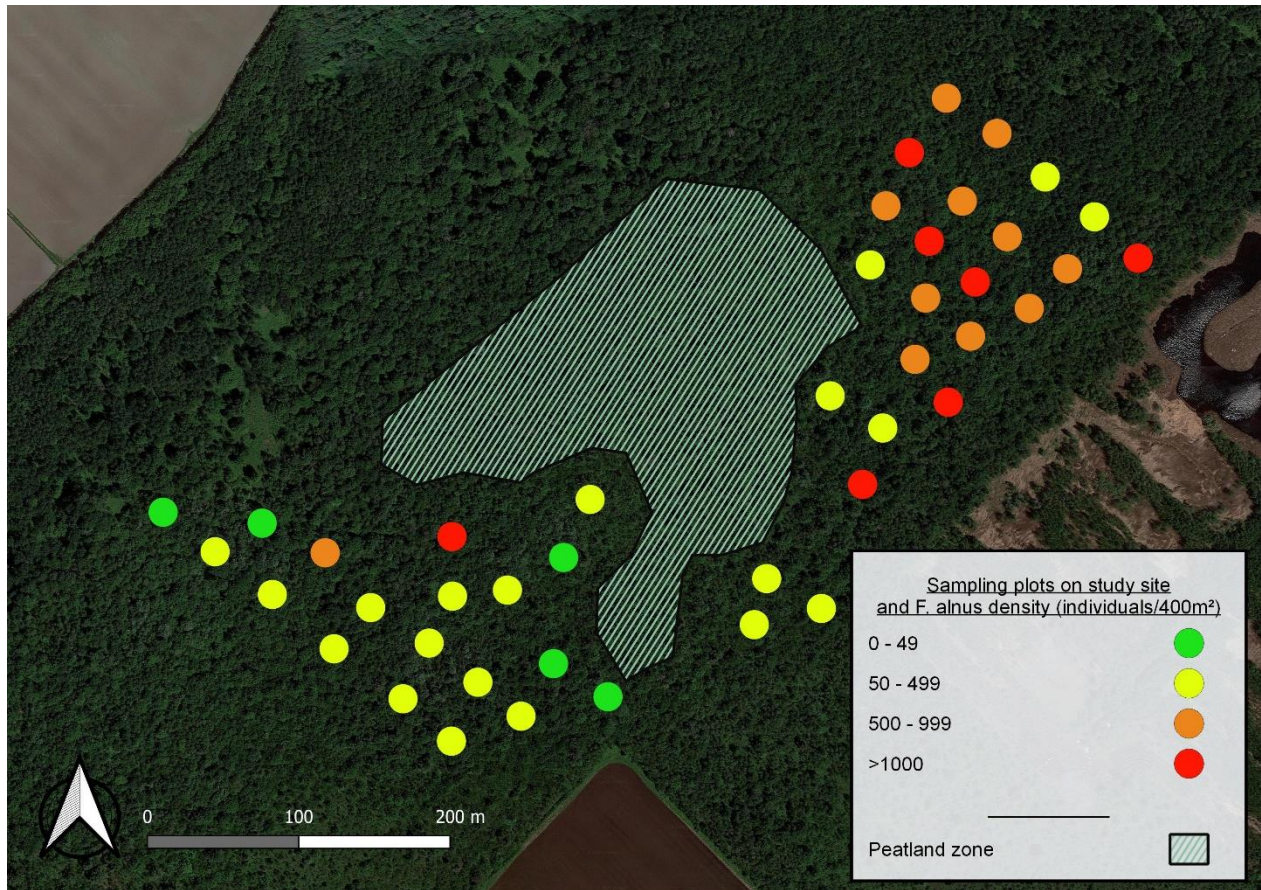


Figure 2.2 Map of the location of all 43 sampling plots on study site. Each plot is associated with a density of *Frangula alnus* (individuals 400 m⁻²). All colors on plots are associated with a density interval to facilitate visualisation. The hatched area represents a peatland zone where no plots were installed because woodland-like environmental characteristics were prioritized. Source: Gabrielle Roberge and GoogleMap (2022).

2.2.2 Understory plant characterization

The understory plants (height < 1 m) were selected for our analyses because they are the most likely to suffer from shading by *Frangula alnus* (Fagan & Peart, 2004; Frappier et al., 2003; Hamelin et al., 2017; Kaul & Wilsey, 2021; Kumar Rai & Singh, 2020; Lavoie, 2019). The estimation of foliage cover to the nearest 5 % for each species of vascular plant in the understory layer was determined in four 1 m² circular plots and averaged on 1 m² (Braun-Blanquet, 1932, 1951). Adult individuals of *Frangula alnus* (height > 1 m) were counted in 5 m² plots (when density was high) and in 50 m² plots (when density was low) to estimate density on 1 m². All plants were sampled from June to August 2020 and identification was done in the field

(Leboeuf, 2016). A sample and a photograph of unidentified individuals were collected for identification in the laboratory using the *Flore Laurentienne* (Marie-Victorin, 1995). A ratio of each species to total understory plant cover was calculated and used as a metric to assess our hypotheses on understory plant diversity.

2.2.3 Saprophagous macroarthropod sampling

Multi-Pher pitfall traps of 20.5 cm height and 10 cm in diameter (Jobin and Coulombe, 1988) were used to collect saprophagous macroarthropods and were installed in the center of each plot in early June, two weeks prior to activating traps, to minimize any disturbance related to digging (Schirmel et al., 2010). The traps contained 100 ml of 50 % ethanol for preservation and were conserved in a 70 % ethanol solution once in the laboratory. As communities may change over the season, two 15-days and one 14-days harvests were carried out, and collects were on July 1st, July 29th, and August 27th for a total trapping effort of 44 days. Due to wildlife disturbances and technical issues, data from five traps in the first sampling and three traps in the third sampling were removed from our analyses. Despite the shortcomings of this method reported by several authors (Brown & Matthews, 2016; Duelli et al., 1999; Topping & Sunderland, 1992), capture with pitfall traps is still one of the most effective and economical ways to make a comparative assessment of edaphic arthropods (Brousseau et al., 2019; Gerber et al., 2008; Sabu et al., 2011; Schirmel et al., 2010; Schuh & Larsen, 2015). All millipedes and woodlice were counted and identified to species level (Borror et al., 1992; Brousseau, n.p.; Langor et al., 2019; Shelley, 2002; Shultz, 2018). Some juvenile Parajulidae could not be identified to species because their secondary sexual characteristics (gonopods) were not developed. After identification, all arthropods were kept in the dark and at room temperature in 80-90% ethanol. Since we were interested in the overall effect on saprophagous macroarthropods, total abundance was used to calculate diversity indices, and the average of their abundance was used for analyzing community structure.

2.2.4 Environmental characterization and measurements

Several environmental variables, such as soil temperature at ground level, humidity, pH, tree canopy cover, litter biomass, and leaf species ratio were collected because they are known to have an impact on ground-dwelling and soil arthropod communities (David & Handa, 2010; Jass & Klausmeier, 2000; Noël & Séchet, 2007; Schuh & Larsen, 2015; Shakir & Ahmed, 2015). HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA) were placed on the ground, under the leaf litter layer, in the center of 24 plots and recorded the temperature every 2 hours from June 11th to August 28th. Soil pH was measured once (3 replicates) in the summer with a pH10 Ecosens probe (YSI Inc., Yellow Springs, OH, USA) and soil moisture

content was measured (3x at less than 1 m from the plot center) with a Field Scout TDR 300 moisture meter (Spectrum Technologies, Inc., Aurora, IL, USA) with 7.6 cm rods. No strong rainfall was recorded within 24h before humidity sampling. An estimate of tree canopy cover percentage to the nearest 5 % was also made for each of the plots (Braun-Blanquet, 1932, 1951). After leaf fall in autumn, a harvest of three quadrats of litter (15cm x 15cm) per plot was carried out and the samples were compiled and dried at 35 °C for 4 days. The dry biomass was used to sort the different species and obtain the composition of the leaf essence in the litter. The average ambient temperature for the summer of 2020 was 20.62 °C and the average precipitation was 75.6 mm (EnvironnementCanada, 2021; WeatherSpark, 2021). Heavy rainfalls were measured during the first arthropod sampling period on June 23rd and 24th (Max = 27 mm). But generally, trapping days had little rain and were mostly sunny or cloudy (WeatherSpark, 2021).

2.2.5 Statistical analysis

To get a general portrait of the environmental conditions on our site following the gradient of *F. alnus*, linear regression tests were carried out: only the pH and the percentage of woody debris cover showed variation across the site gradient (Table 2.1). Redundancy analyses (RDA) were used to explore community structure across plots for both plants and soil macrofauna. To analyze plant communities and provide better visualization, rare species (<5 % average cover and found in less than 5 % of plots) were removed. Plant cover ratios were transformed (Hellinger) to minimize the effect of extreme species and double zeros (Anderson et al., 2006; Legendre & Gallagher, 2001; Zeleny, 2021). For the analysis of saprophagous macroarthropods, species with fewer than 5 individuals and unidentified juvenile individuals (Parajulidae) were also removed. Mean abundance of saprophagous macroarthropods across all trapping days was used and log-transformed to avoid the *horseshoe effect* (Anderson et al., 2006). Along with density of *F. alnus*, other environmental factors that are likely to influence community structure were used as constraint variables in the RDA. For understory plants, soil moisture, pH, and canopy cover were used. For saprophagous macroarthropods, percentage of *F. alnus* in leaf litter, the effective number of understory plant species, woody debris cover, and litter biomass were used. For both groups, constraint variables were standardized and centered on 0.

Table 2.1 Linear regression model outputs of the environmental variables associated with density gradient of *F. alnus* to assess an overview of the environmental conditions across our study site. Some variables that are most likely to influence the density of *F. alnus* were used as independent variables, such as tree canopy cover (%) and pH. Other variables that might be influenced by *F. alnus*, such as soil humidity (%), leaf litter biomass (g m⁻²), ground-level temperature (°C), and woody debris cover (%) were used as dependent variables to determine if they varied across the gradient of *F. alnus*.

Dependant variable	Independant variable	Mean ± SD	Estimate	SE	T-value	R ²	p-value
<i>F. alnus</i> density (nb m ⁻²)	Canopy cover (%)	58.95 ± 13.30	-0.009	0.006	-1.360	0.043	0.181
	pH	4.00 ± 0.40	-0.482	0.206	-2.344	0.118	<0.05 *
Humidity (%) ¹	<i>F. alnus</i> density (nb m ⁻²)	20.46 ± 10.80	-0.034	0.092	-0.364	0.003	0.718
Leaf litter biomass (g m ⁻²) ¹		269.26 ± 65.90	0.238	0.267	0.893	0.019	0.377
Ground temperature (°C) ¹		20.15 ± 0.48	0.086	0.077	1.122	0.054	0.274
Woody debris cover (%) ¹		13.80 ± 6.50	0.510	0.083	6.16	0.481	<0.001 ***

¹ Square root transformation to fit the linear regression model conditions

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$

To test the potential effect of *F. alnus* on various community metrics of native understory plants (including rare plants) and saprophagous macroarthropods, linear regression models using the density of adult *Frangula alnus* as an explanatory variable were used to explore species richness (S), abundance, the effective number of species, Shannon-Wiener index (H') and Pielou's evenness index (J'). The Shannon-Wiener index was obtained from the formula $H' = -\sum P_i \ln P_i$, where P_i corresponds to species cover proportion i on the total cover (for understory plants) and individual number proportion per species i (for millipedes and woodlice). Pielou's evenness was obtained with this formula: $H'/\ln(S)$. The effective number of species is an index based on the Shannon-Wiener's index and is applied with this formula: $e^{H'}$ (Jost, 2006). For native understory plants, the abundance and evenness index were square root transformed to meet the conditions of linear models. Evenness also had one extreme data retrieved (plot L4) to fit the normality conditions of the linear model, as determined with diagnostic tests. For saprophagous macroarthropods, percentage of *F. alnus* in the litter and the effective number of plant species were also used as an explanatory variable, in addition to the different environmental factors likely to interact with this group (litter biomass (mg m⁻²), pH, humidity (%) and woody debris (%)). All analyses and data processing were carried out with the R program version 4.0.4 (R core Team 2021) with the *vegan* package (Oksanen et al., 2007)

2.3 RESULTS

2.3.1 Native understory plants

A total of 54 species of understory plants were found throughout the study site (Table 2.2). Among the most common species, saplings of red maple (*Acer rubrum*) accounted for around 11% of the total vegetation cover across all study plots, making it the second most abundant understory plant after *F. alnus*. The most abundant shrubs were species from Ericaceae (*Rhododendron canadense*, *Vaccinium angustifolium*, and *Kalmia angustifolia*) and Rosaceae (*Aronia melanocarpa*) families. Each species was represented on average between 3 and 8 % of total vegetation cover (Table 2.2). The most abundant herbaceous plant species was *Maianthemum canadense* with an average cover of around 4% as well as four species of pteridophytes with a combined average cover of around 12 % (*Dryopteris spinulosa*, *Onoclea sensibilis*, *Osmunda claytonia*, *Osmunda cinnamomea*). The rare species (n = 27) altogether covered on average less than 5% of the total vegetation cover. Other invasive alien plant species were also reported including *Phragmites australis* and *Galeopsis ladanum*. They represented less than 3% of the vegetation cover and were found in less than 5 % of the sampling stations (Table 2.2). We also observed a general decrease in total native plant abundance across the gradient of *F. alnus*, where the highest abundance was observed when *F. alnus* between 1 and 2 individuals m⁻² (Fig. 2.4a, R² = 0.11, p < 0.05).

Table 2.2 Dominant understory plant species: trees, shrubs, and herbaceous plants (>5 % presence in plots and >5 % vegetation cover) in all 43 plots on our site. Data were collected in 4 circular plots of 1 m² (averaged over 1 m²) for all 43 sampling plots. Shade tolerance, frequency (percentage of presence in plot) and average cover (percentage) of total vegetation for each of dominant understory plant species.

Family	Genre	Species	Shade tolerance	Frequency	Average cover ± SE
<i>Native and cosmopolitan species</i>					
Trees					
Rosaceae	<i>Prunus</i>	<i>virginiana</i>	Tolerant ^{4,13}	16.3	0.6 ± 0.3
Sapindaceae	<i>Acer</i>	<i>rubrum</i>	Medium ⁸	100	11.2 ± 1.4
Salicaceae	<i>Populus</i>	<i>tremuloides</i>	Intolerant ^{4,6}	30.2	0.5 ± 0.1
Shrubs					
Aquifoliaceae	<i>Ilex</i>	<i>mucronata</i>	Tolerant ³	34.9	1.4 ± 0.3
Caprifoliaceae	<i>Viburnum</i>	<i>cassinoides</i>	Tolerant ⁴	41.9	2.7 ± 0.7
Cornaceae	<i>Cornus</i>	<i>alternifolia</i>	Tolerant ^{11,13}	7	1.1 ± 0.7
Ericaceae	<i>Kalmia</i>	<i>angustifolia</i>	Intolerant ⁸	48.8	3.4 ± 0.8
	<i>Rhododendron</i>	<i>canadense</i>	Tolerant ⁹	55.8	6.2 ± 1.4
	<i>Vaccinium</i>	<i>angustifolium</i>	Intolerant ⁴	58.1	6.2 ± 1.2
	<i>Chamaedaphne</i>	<i>caliculata</i>	Intolerant ⁶	9.3	0.3 ± 0.2

Rosaceae	<i>Aronia</i>	<i>melanocarpa</i>	Intolerant ⁴	88.4	8.3 ± 1.0
	<i>Rubus</i>	<i>occidentalis</i>	Tolerant ¹⁰	14	1.8 ± 1.2
	<i>Rubus</i>	<i>allegheniensis</i>	Intolerant ¹	9.3	0.6 ± 0.3
	<i>Rubus</i>	<i>pubescence</i>	Tolerant ⁴	44.1	5.1 ± 1.4
	<i>Rubus</i>	<i>hispidus</i>	Tolerant ¹³	16.3	1.8 ± 0.9
	<i>Rubus</i>	<i>Idaeus</i>	Intolerant ⁴	16.3	2.3 ± 1.0
	<i>Spirea</i>	<i>latifolia</i>	Medium ⁷	76.7	3.5 ± 0.6
Herbaceous					
Asparagaceae	<i>Maianthemum</i>	<i>canadense</i>	Medium ⁴	69.8	4.3 ± 0.9
Osmundaceae	<i>Osmunda</i>	<i>claytonia</i>	Tolerant ¹³	7	0.7 ± 0.5
Polypodiaceae	<i>Dryopteris</i>	<i>spinulosa</i>	Tolerant ¹³	20.9	4.3 ± 1.9
	<i>Onoclea</i>	<i>sensibilis</i>	Medium ⁴	7	1.1 ± 1.0
	<i>Osmunda</i>	<i>cinnamomea</i>	Tolerant ¹³	11.6	1.2 ± 0.8
Primulaceae	<i>Lysimachia</i>	<i>borealis</i>	Tolerant ¹³	62.8	3.0 ± 0.8
Vitaceae	<i>Parthenius</i>	<i>quinquefolia</i>	Tolerant ²	23.3	1.8 ± 0.7
Exotic species					
Lamiaceae	<i>Galeopsis</i>	<i>ladanum</i>	Medium ¹²	2.3	< 0.1
Poaceae	<i>Phragmites</i>	<i>australis</i>	Intolerant ¹³	4.7	< 0.1
Rosaceae	<i>Frangula</i>	<i>alnus</i>	Tolerant⁵	93	20.5 ± 3.0
Rare species: 27					<5%
Richness of native species: 51					
Total richness: 54					

Note : references for plant's shade tolerance are available in the appendix section (see Appendix 1.1.2)

2.3.2 Native understory plant communities

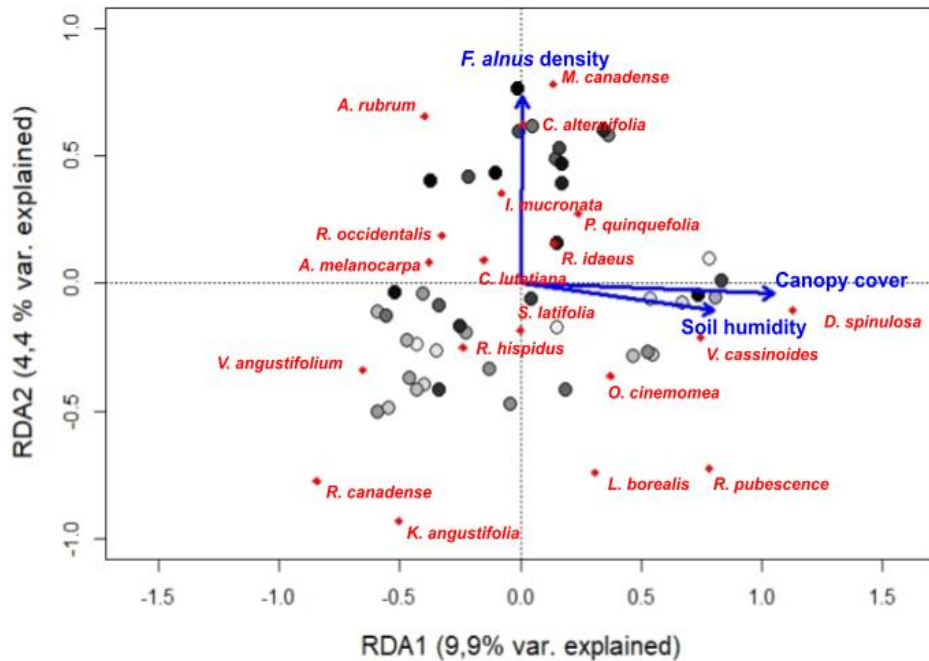


Figure 2.3 Redundancy analysis (see statistical output in Appendix 1.1.3) of all native understory plant species (<1 m in height) according to each sampling plot. Density of *F. alnus* is represented by a gray gradient to visualize the degree of invasion, whereby pale plots have a lower density (0 individual m⁻²) and gradually increase to dark for high density plots (>4 individual m⁻²). Plant species, in red, have been centered and transformed (Hellinger). Constraint variables (canopy cover, average humidity, average pH, and adult density of *F. alnus*), in blue, have also been standardized, centered on 0.

Our redundancy analysis model for understory plant community composition only explained around 15 % of the variation along the two first axes (Fig. 2.3, 16.8 % total var. explained). Nonetheless, we still observed that community composition was particularly alike in plots with high density of *F. alnus*, comprised mostly of shrub species such as *Cornus alternifolia*, *Ilex mucronata*, *Rubus occidentalis*, and *Parthenocissus quinquefolia*, herbaceous species like *M. canadense* and *Circea lutetiana* and tree seedlings of *A. rubrum*. But as density of *F. alnus* only explained a low percentage of variation (4.4 %), this observation is therefore mostly driven by other environmental factors, such as soil humidity and tree canopy cover, which are both associated to the axis 1 and explain more than twice as much variation (9.9 %). Moreover, we can generally observe that shade-tolerant plant species were present on both ends (low and high density) of the *F. alnus* density gradient. Conversely, peatland species like *K. angustifolia*, *R. canadense*, *V. angustifolium*, *Rubus hispidus*, and *Spiraea latifolia* were mainly associated with plots with lower tree canopy cover and lower humidity. These species are mostly shade-intolerant and tend to prefer

higher luminosity and soil humidity, and more acidic organic soils. Humidity levels and tree canopy didn't generally vary across our plots (Table 2.1), so variation in the understory plant communities is more likely explained by other environmental variables we didn't measure in our study.

2.3.3 Native understory plant diversity

Table 2.3 Linear regressions of density of *F. alnus* (individual m⁻²) as predictive variables on five diversity index of understory native plant species (height < 1 m). Evenness index and total abundance have been transformed (square roots) to fit linear model conditions. All plant diversity indices are based on the ratio of cover average (to the closest 5%, on 1 m²) of each species on total plant cover.

Dependent variable	Descriptive statistics		Linear model outputs				
	Mean ± SE	Median (Min-Max)	Estimate	SE	T-value	R ²	p-value
Specific Richness (S)	11.4 ± 2.5	11 (7-17)	-0.093	0.331	-0.281	0.002	0.78
Effective number of species	7.1 ± 2.2	6,97 (2.60-12.9)	-0.783	0.264	-2.967	0.177	<0.005 **
Shannon-Weiner index (H')	1.9 ± 0.3	1.94 (0.95-2.56)	-0.129	0.039	-3.316	0.211	<0.005 **
Evenness (J') ¹	0.8 ± 0.11	0.80 (0.39-0.91)	-0.030	0.008	-3.731	0.272	< 0.001 ***
Total abundance of native understory plant species (%) ¹	38.3 ± 16.7	36.90 (9.5-79.45)	-0.392	0.172	-2.276	0.112	< 0.05 *

¹ Square root transformation to fit the linear regression model conditions

* P<0.05; **P<0.005; ***P<0.001

We found a consistent negative response of understory plant diversity along the gradient of *F. alnus* with most diversity metrics (Figure 2.4). Even though there was no influence of *F. alnus* density on species richness (R² = 0.002, p = 0.78), other plant diversity metrics such as the effective number of species (R² = 0.177, p < 0.005), Shannon-Wiener diversity (R² = 0.21, p < 0.005) and Pielou's evenness (R² = 0.26, p < 0.001) all decreased along the *F. alnus* density gradient. Although effects were moderate, models showed that *F. alnus* explained about 17.7 % of the variation in the effective number of species, 21.1 % of the Shannon-Wiener index, and 25.8 % of evenness in the understory native plants found in our system (Table 2.3).

These results suggest a tendency in homogenization of species and a mild, but non-negligible decrease in native plant species diversity when density of *F. alnus* increased at our site (Table 2.3).

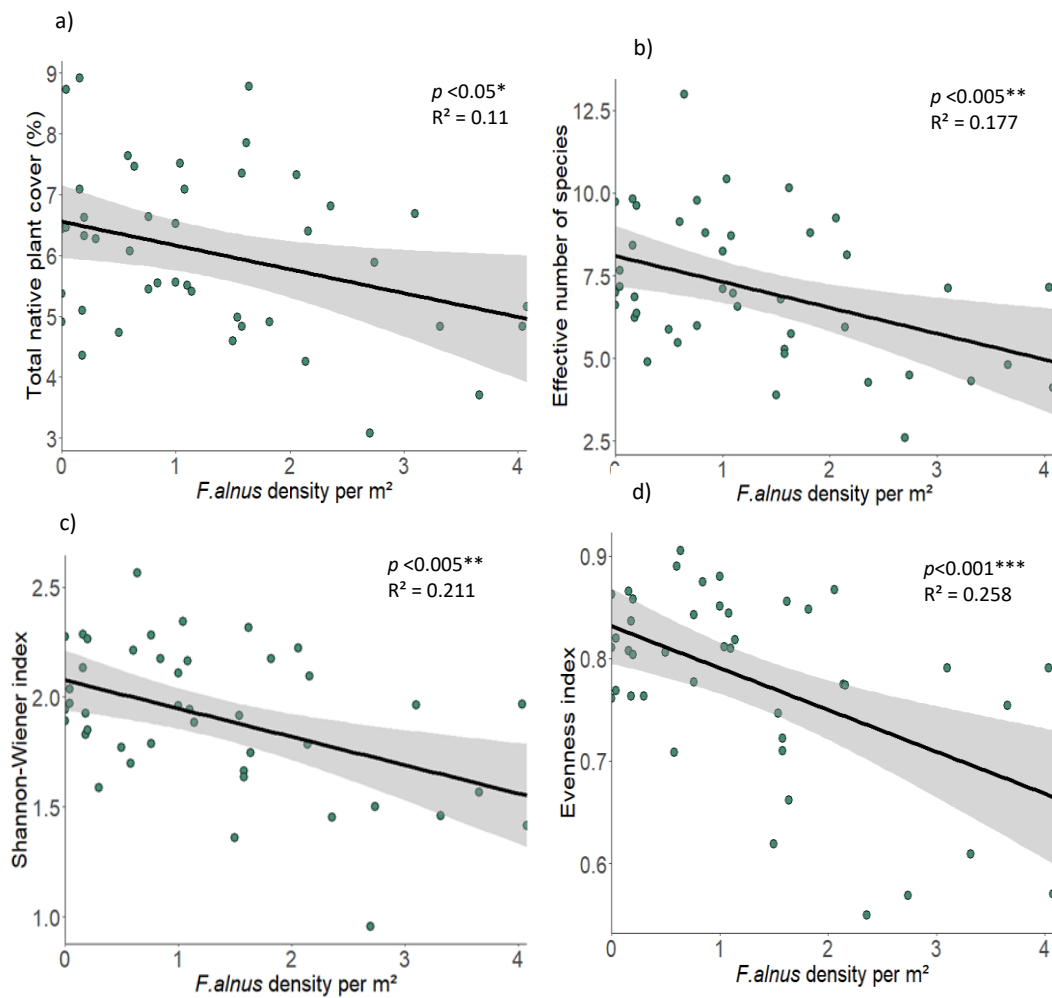


Figure 2.4 Simple linear relationships between the (a) total native understory plant cover (square-root), (b) effective number of native plant species, (c) Shannon-Wiener index, (d) Pielou's evenness index as dependent variables, and density gradient of *F. alnus* (individual m⁻²) as an explanatory variable on the study site.

2.3.4 Saprophagous macroarthropods

Table 2.4 Abundance, age (juvenile or adult), habitat, and origin (native/exotic) for each species of saprophagous macroarthropods captured in the 43 pitfall traps during the summer of 2020 on the site.

Class	Order	Family	Genre and Species	Total abundance	Age (J/A)	Origin (N/E)	Habitat
Diplopodes	Chordeumatida	Cleidogonidae	<i>Cleidogona sp.</i>	2	A	NA	NA
	Julida	Blaniulidae	<i>Choneiulus palmatus</i>	56	A	E	Urban, disturbed habitats ⁵
	Julida	Julidae	<i>Ophiulus pilosus</i> (Newport)	138	A	E	Wetlands, Urban ¹
	Julida	Parajulidae	<i>Uroblaniulus canadensis</i> (Newport)	99	A	N	Open woodland ² , mesic ⁵
	Julida	Parajulidae	<i>Oriulus venustus</i> (Wood)	6	A	N	Open woodland ²
	Julida	Parajulidae	<i>Parajulidae sp.</i>	5	J	NA	NA
	Polydesmida	Polydesmidae	<i>Polydesmus inconstans</i> Latzel	178	A	E	Urban ¹
	Polydesmida	Polydesmidae	<i>Pseudopolydesmus serratus</i>	266	A	N	Mixed forests ⁴
	Spirobolida	Spirobolidae	<i>Narceus americanus</i>	88	A	N	Woodland, Urban ¹
Malacostraca	Isopoda	Trachelipodidae	<i>Trachelipus rathkii</i>	1728	NA	E	Terrestrial, generalist ³

Species richness: 9

Total abundance: 2566

Note: see references for origins and habitats of saprophagous macroarthropods in Appendix 1.1.2

A total of 2,566 saprophagous macroarthropods were collected throughout all sampling periods. A total of 9 species were observed, in which one could only be identified to genus (*Cleidogona sp.*). We also observed 5 juvenile specimens in the Parajulidae family that could not be identified to species (Table 2.4). Overall, total abundance did not vary across the gradient of *F. alnus* (Table 2.5), but we observed different responses according to the species and their characteristics. In the class Isopoda, only the exotic generalist species *Trachelipus rathkii* was observed and was the most abundant (n = 1728). All 8 other species collected were diplopods; three of which were exotic (*Ophiulus pilosus*, *Choneiulus palmatus*, and *Polydesmus inconstans*). *O. pilosus* abundance increased slightly following the gradient of *F. alnus* whereas *C. palmatus* and *P. inconstans* were relatively stable (see Appendix 1.1.4). Moreover, some species were only found in very low abundance, such as *Cleidogona sp.* (n=2) and *O. venustrus* (n=6) (Table 2.4). Native species *U. canadensis* and *N. americanus* generally had lower abundance in high *F. alnus* density plots (see

Appendix 1.1.5). *N. americanus*, *C. palmatus*, *P. inconstans*, and *O. pilosus* are synanthropic and adapted to disturbed and urban areas (Jędryczkowski, 1982; Shelley, 1988; Sierwald et al., 2019).

2.3.5 Saprophagous macroarthropod community composition

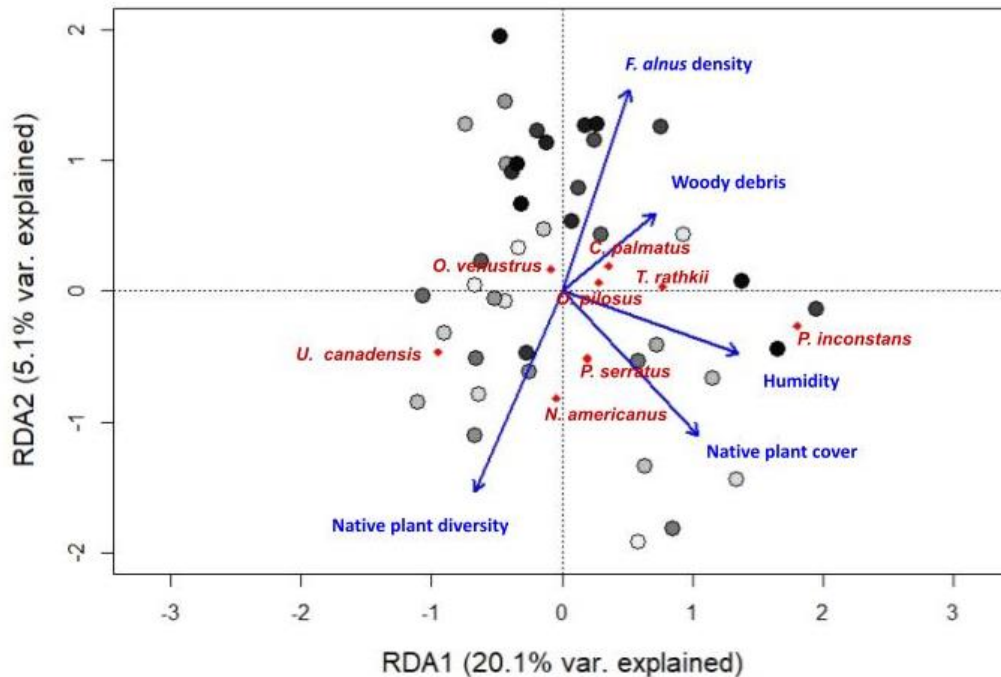


Figure 2.5 Redundancy analysis (see statistical output in Appendix 1.1.4) of saprophagous macroarthropod communities across sampling plots. Density of *F. alnus* is represented by a gray gradient to visualize the degree of invasion, whereby pale dots have a lower density (0 individual m⁻²) and gradually increase to darker dots for high density plots (> 4 individual m⁻²). The species, in red, have been transformed (log) to minimize the effect of very abundant species and the horseshoe effect. Constraint variables (soil humidity (%), woody debris cover (%), plant diversity (effective number of native plant species), and native understory plant cover (%)), in blue, were standardized, centered on 0, and vectors were scaled (*1.2) for better visualization.

Overall, selected variables generally predicted composition of saprophagous macroarthropod communities (Fig. 2.5, 32.1 % total var. explained). But density of *F. alnus* had a weak influence on variation in community composition as it was associated mostly with axis 2 of the RDA (5.1%), compared to other vectors that were mostly associated with axis 1, such as native plant cover, woody debris cover and soil humidity (20.1% var. explained). Nonetheless, some native species (*Uroblaniulus canadensis*, *Narceus americanus*, and *P. serratus*) were associated with plots with higher native understory plant diversity and less *F. alnus* density. Also, smaller native species such as *P. inconstans* and *U. canadensis* were influenced by humidity and woody debris cover. Indeed, *U. canadensis* was associated with plots with lower humidity

levels and more understory native plant diversity, whereas *P. inconstans* was particularly found where woody debris cover, and soil humidity were higher. Exotic *T. rathkii* and *C. palmatus* were also associated with these environmental vectors, but not as much. No species were strongly associated with high *F. alnus* density as we generally observed that most species were more represented in plots where *F. alnus* density was lower. Similar to our observations with understory plants, these results suggest that saprophagous community composition was unrelated to *F. alnus* density and that other environmental variables were more important drivers of community structure.

2.3.6 Saprophagous macroarthropod diversity

Table 2.5 Descriptive statistics and linear regression outputs of density of *F. alnus* (individual m⁻²) as predictive variables on five community indices (species richness, effective number of species, Shannon-Wiener index, and evenness index) for saprophagous macroarthropod species. Abundance of millipedes and woodlice have been transformed (square-root) to fit linear model conditions. All arthropod data are based on the average of total abundance of three collects within summer of 2020.

Dependent variable	Descriptive statistics		Linear model outputs				
	Mean ± SE	Median (Min-Max)	Estimate	Std error	T-value	R ²	p-value
Species richness ¹	4.47 ± 0.13	5 (2-6)	-0.27995	0.1070	-2.616	0.1431	<0.02*
Effective number of species	2.59 ± 0.11	2.49 (1.24-4.14)	-0.19505	0.09306	-2.096	0.100	<0.05*
Shannon-Wiener index (H')	0.91 ± 0.04	0.914 (0.26-1.42)	-0.09680	0.03677	-2.633 7	0.1446	<0.02*
Evenness index (J')	0.60 ± 0.02	0.612 (0.216-0.881)	-0.05082	0.02005	-2.535	0.1355	<0.02*
Total abundance ²	20.39 ± 1.8	20.3 (4.3-52.6)	0.2541	0.1696	1.498	0.05191	0.142

¹ Species richness' variation is very low (from 2 to 6 species), must be interpreted with caution.

² Square root transformation to fit the linear regression model conditions.

* P<0.05; **P<0.005; ***P<0.001

Similar to what was observed with understory plants, an increase in *F. alnus* was associated with a decrease in all indices of saprophagous macroarthropod diversity (Fig. 2.6, Table 2.5). Plots with a higher density of *F. alnus* showed a decrease in the effective number of detritivore species ($R^2 = 0.10$, $p < 0.05$), Shannon-Wiener index ($R^2 = 0.15$, $p < 0.02$), and evenness ($R^2 = 0.14$, $p < 0.02$). Species richness also was negatively impacted ($R^2 = 0.14$, $p < 0.02$), but since the total number of species per plot ranged only from 2 to 6, data could not be normalized to fit model conditions, and therefore must be interpreted with caution. Similar as to observed with understory plants, the Shannon-Wiener and evenness indices suggested a tendency for decreased diversity and a homogenization of saprophagous microarthropod communities as density of *F. alnus* increased, but effects were weak (Table 2.5).

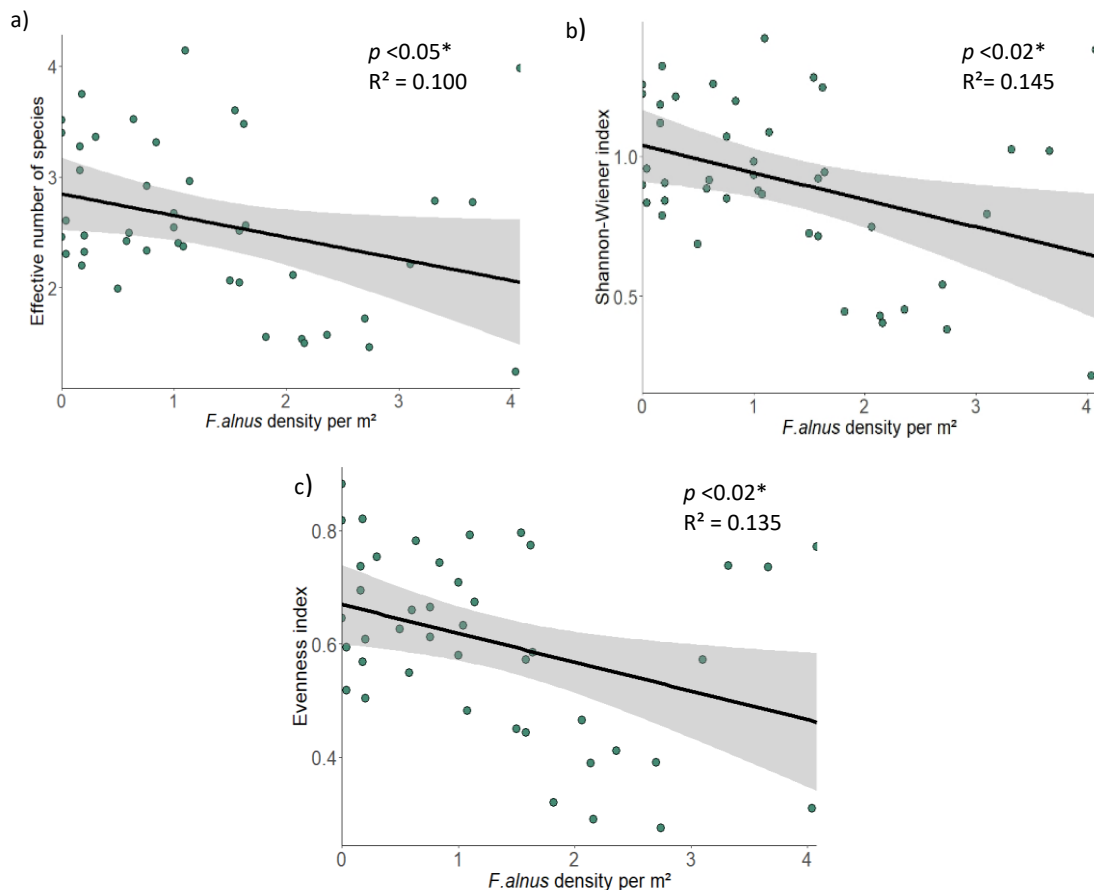


Figure 2.6 Simple linear relationships between the (a) the effective number species, (b) Shannon-Wiener index, (c) evenness index as dependent variables of saprophagous macroarthropods, and density of *F. alnus* (individual m⁻²) as an explanatory variable on the study site.

Other environmental factors, such as *F. alnus* leaf ratio in litter and understory plant diversity (effective number of species) were considered to understand possible mechanisms affecting saprophagous macroarthropod communities. Neither a reduction in understory native plant diversity nor an increase in *F. alnus* ratio in leaf litter influenced saprophagous macroarthropod diversity (Appendix 1.1.5). A decrease in effective number of understory plant species did not interact with the effective number of saprophagous macroarthropod species ($R^2 = 0.03$, $p = 0.235$) nor their abundance ($R^2 = 0.001$, $p = 0.824$). Results excluding the overrepresented species *T. rathkii* indicated that this species was the most powerful driver of the observed effects, as no significant difference in any diversity indices were observed with its removal (Appendix 1.1.6).

2.4 DISCUSSION

Numerous studies have reported that IAPS alter the community composition and decreases the diversity of native plants and invertebrates by altering microbial communities, abiotic and, biotic components in their invaded ecosystems (Callaway et Maron, 2006; Coyle *et al.*, 2017; Kumar Rai et Singh, 2020; Lalk *et al.*, 2021; Lavoie, 2019; Litt *et al.*, 2014). Since *F. alnus* has the ability to modify understory environmental conditions and some authors reported that it could decrease native plant diversity (Converse, 1984; Fagan et Peart, 2004; Stokdyk et Herrman, 2014), we hypothesized that an increase in density of *F. alnus* would alter community composition and lower the diversity for native understory plants and saprophagous macroarthropods. We did not find a strong alteration of both community composition due to increasing *F. alnus*, but our results did show that it had a moderate negative effect on some diversity metrics for understory plants.

2.4.1 Understory native plant species

Invasion by *F. alnus*, like other IAPS, has been associated with plant community changes and loss of plant diversity (Fagan et Peart, 2004; Frappier, Brian *et al.*, 2003; Possessky *et al.*, 2000). Although we observed a gradual dominance and homogenization by *F. alnus* in our system, also observed by Reinartz and Kline (1988), in our study, species richness (Table 2.3) and variation in community species structures (Figure 2.3) were poorly explained by density of *F. alnus*. Some studies found negative impacts of *F. alnus* on young tree species (Frappier, B. *et al.*, 2004; Hamelin *et al.*, 2016), but no difference was observed in our system on tree seedlings. However, we still observed a decrease in native understory plant diversity indices when density of *F. alnus* was increasing, especially for shade-intolerant peatland species such as *V. angustifolium* and *K. angustifolia* (Figure 2.3). These observations were non-negligible, but still not as pronounced as expected. In their study, Hedja *et al.* (2009) observed that some IAPS (i.e., *Fallopia spp.* and *Heracleum*

mantegazzianum) have stronger negative impacts than others on plant community and richness. Out of a total of 13 IAPS tested, only 5 showed an obvious adverse effect on the native plant species. It may thus not be surprising that *F. alnus*, like other IAPS are less competitive than others, explaining why we only observed a weak decrease in the effective number of species, Shannon-Wiener index, and evenness index. Our results were also similar to a recent experimental study on *F. alnus* that also showed equivocal results. Hamelin *et al.* (2017) observed better growth, but not significant, of three herbaceous plants in plots without *F. alnus*. Other studies also support the interpretation that *F. alnus* is not a severe problem for plant diversity, by suggesting an increase in native plant richness (Houlahan et Findlay, 2004; Possessky *et al.*, 2000) or no effect on herbaceous plants (Frappier, B. *et al.*, 2004). The small decrease in diversity and change in relative abundance of the understory plant community maybe due to *F. alnus* being less competitive compared to other invasive plant species. For instance, Aguilera et al (2010) reported strong negative effects in their study on invasive species *F. japonica*, wherein some plots without *F. japonica* could have up to 10 times more native species and an effective number of species almost 5 times greater outside the invaded plots. Kedzie-Webb *et al.* (2001), studying the allelopathic species *Centaurea maculosa* also measured a pronounced decrease in native plant density, richness, abundance, and Shannon-Weiner index. Mechanisms that can influence species competitiveness could include efficient dispersal strategies, positive plant-soil feedbacks, plasticity, and allelopathy (Klionsky et al., 2011; Lavoie, 2019; Roiloa et al., 2020). Unfortunately, it is still difficult today to identify which specific mechanisms make an IAPS more competitive than others in natural environments (Roiloa et al., 2020).

2.4.2 Saprohagous macroarthropods

According to the *resource specialization hypothesis*, loss of diversity and alterations in the plant species community should also as a corollary, lower the diversity of the primary consumers (Brousseau et al., 2019; Litt et al., 2014; McCary et al., 2016; Schuh & Larsen, 2015; Southwood et al., 1979). Probably as a result of the decrease in understory plant diversity, we also observed a weak decrease in saprophagous macroarthropod diversity (Table 2.5). But when over representing data from *T. rathkii* were excluded from our analysis, no effects were observed. Moreover, when modelled individually, *T. rathkii* was found to generally increase when density of *F. alnus* increased ($p < 0.05$, $R^2 = 0.08$, Appendix 1.1.7). This may suggest a tendency to homogenization associated to *T. rathkii*, which is not surprising, as it is a generalist exotic species that tends to thrive in disturbed environments and is one of the 10 most abundant Oniscidea species in North America and found in near bogs (Brigić et al., 2017; Jass & Klausmeier, 2000; Magura et al., 2008). The disproportionate abundance of this group and the few species observed in total could also signify that we need to include other types of soil invertebrates in future studies, as exotic *T. rathkii* is

confounding the results (Gerlach et al., 2013). In following, we also observed that all exotic species either increased a little in abundance or were unaffected when *F. alnus* increased in density (Appendix 1.1.4). These exotic species are known to be either generalist or resilient to disturbance, suggesting they might be more resistant to disturbance (Richmond et al., 2005; Shelley, 1988). We also observed that native species, such as *U. canadensis* and *N. americanus* were associated with plots that are lower in *F. alnus* density and higher understory plant diversity, implying that these species could be more sensitive to invasion from *F. alnus* (Appendix 1.1.5). Nonetheless, due to molting and chronic desiccation, it has been observed that *N. americanus* is less active around mid-August in certain places in eastern north America (O'Neill, 1968). More input considering seasonal effects should therefore be considered before drawing any conclusions. Overall, the fact that saprophagous macroarthropods were only weakly affected by *F. alnus* is still congruent with other studies. According to the results of a global assessment by Pyšek et al. (2012), animals are less inclined to react to a species invasion compared to autotrophs.

In our community composition, we showed that the strongest drivers were environmental factors such as soil humidity and woody debris (Figure 2.5). Moreover, no mechanisms responsible for the decrease in diversity could be identified within our selected variables, as *F. alnus* ratio in litter content and understory native plant diversity were both inconclusive variables explaining the diversity loss in saprophagous macroarthropod in our system. Schuh & Larsen (2015), with *R. cathartica*, had a similar situation, where they found an adverse impact on ground-dwelling arthropods but could not identify the responsible mechanism. They hypothesized that changes in the litter biomass and chemistry, nutrient content, and micro-detritivores community might be the cause of their results. Something similar could be interpreted with our results with variables we didn't measure, such as carbon, nitrogen, ligneous content, and other trophic levels. We know that *F. alnus* alters nitrogen mineralization in soil and microbiotic components (Stokdyk & Herrman, 2014, 2016), but no other information is available on its leaf litter characteristics, which makes it difficult to speculate about its interactions with saprophagous macroarthropods. To provide additional input on *F. alnus*, more research on leaves characteristics and components would be pertinent. Moreover, an interesting pathway for future investigations could be through study of functional traits, which allow better generalization than the taxonomic approach on covariability between the consumers and their resources (Brousseau et al., 2018)

2.4.3 Our system

There is a strong consensus on how invasive species are one of the biggest causes of biodiversity loss (IPBES, 2019), but equivocal results, similar to ours, have been observed by other authors when it comes to the impacts of IAPS (Davis & Thompson, 2000; Diekmann et al., 2016; Frappier et al., 2003; Mills et al., 2009; Qureshi et al., 2021; Ricciardi & Cohen, 2007; Robertson et al., 2011). Indeed, not all species have the same level of impact on native ecosystems, and not all the ecosystems and groups of organisms react the same to invasion (Brousseau et al., 2021; Litt et al., 2014; Pyšek et al., 2012; Robertson et al., 2011). As stated by Pyšek *et al.* (2012) in their global assessment, around 63.3% of invasive plants are recorded as having a significant negative impact on the system they invade. Since *F. alnus* seems less competitive, it could be less problematic for biodiversity compared to other IAPS in some sites and ecosystems. However, we also suspect that invasion by *F. alnus* on our study site might be too early to provoke strong changes in communities of both our study groups. A relevant observation in our results was that for our understory plant diversity, plots with density of *F. alnus* higher than 1.5 individuals per m² had a noticeable decrease in the average of the effective number of species (Figure 1.4). Because older growths tend to have even-aged dense thickets (Converse, 1984), it would not be surprising that obvious negative impacts happen at a higher density threshold or later in the invasion process, as explained for other invasive species by Panetta & Gooden (2017). Since Mills *et al.* (2009) barely observed an impact of *F. alnus* after 15 years in a similar ecosystem, we could suspect that after 26 years, changes are starting to be noticeable, but not extremely pronounced. Our results can thus be viewed as consistent with the equivocal interpretations found in the literature and can be interpreted as having little effect on both our study groups, even if we observe tendency of a gradual dominance of *F. alnus* on our site. This suggests that invasiveness of *F. alnus* does not necessarily correlate with the severity of its impact, which was also the statement of Ricciardi and Cohen (2007) on IAPS.

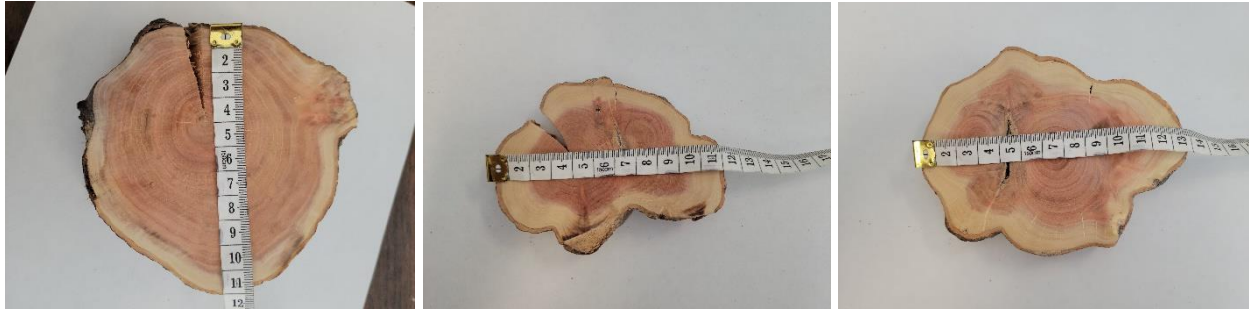
2.4.4 Challenges and limits

Even within one site, there are many variables that cause variation in species community composition due to heterogeneity. Even if most of our tested variables did not vary along the *F. alnus* gradient on our site (Table 2.1), in an ecological system, controlling variables is challenging as they are numerous and interact with each other. Diekmann *et al.* (2016) also observed weak negative results on plant richness from IAPS *Impatiens glandulifera* and *Impatiens parviflora*. They suggested that the multitude of environmental variables in a field experiment makes it difficult to correlate and extrapolate the mechanisms within the interaction of IAPS and plant diversity, which is also something we encountered within our study. Also,

some bias could originate from our vegetation sampling methods. In the future, it would be preferable that plot size were larger (Archaux et al., 2007). Moreover, although our gradient approach provided more spatial input, having multiple study sites could give us a better general understanding of the interaction of *F. alnus* with understory plants and saprophagous macroarthropods. As observed by Qureshi *et al.* (2021) and Brousseau et al. (2021), communities in different sites and ecosystems can react significantly differently when invaded by an IAPS. We also think that including a seasonal timeline in our analysis could offer pertinent information about presence of certain species depending on the time of the season. Finally, one challenge we came upon was the lack of consistency in scientific literature when it comes to assessing IAS. As stated by multiple authors, studying IAPS is very complicated because multiple agencies are working on this issue (Barney & Tekiela, 2020; Barney et al., 2013; Matthews et al., 2017; Ricciardi & Cohen, 2007). A uniformized impact metric, as proposed by Barney *et al.* (2013) would therefore be adequate for further investigation.

2.5 APPENDIX

1.1.1 Horizontal cuts of biggest *F. alnus* specimens found on site in 2019



Horizontal cuts of 3 biggest *F. alnus* specimens found on site in a previous sampling campaign, in 2019, by a management team of Université du Québec à Montréal.

1.1.2 References for table 2.2 and 2.4

References for Table 2.2 used to determine shade tolerance for each of the understory plant species that had > 5 % average cover and were found in more than 5 % of all 43 plots on the study site. Each number corresponds to the reference used for each species in the Table 2.2.

1. Bajcz (2014)
2. Carter *et al.* (1989)
3. González *et al.* (2014)
4. Humbert (2006)
5. Lavoie (2019)
6. Marie-Victorin (1995)
7. Stanton *et al.* (2010)
8. Moizuk & Livingston (1966)
9. Pellerin *et al.* (2008)
10. Peterson & Pickett (1995)
11. Petrukaitis & Gudzinikas (2020)
12. Plant For a Future (2022)
13. USDA Plant Database (2022)

References for Table 2.4 used to determine the origin and habitat of identified species of saprophagous macro arthropods in all 43 the plots on the study site. Each number corresponds to the reference used for each species in the Table 2.4.

1. Shelley (1988)
2. David & Handa (2010)
3. Magura, Hornung & Tóthmérész (2008)
4. Sierwald *et al.* (2019)
5. Jędryczkowski (1982)

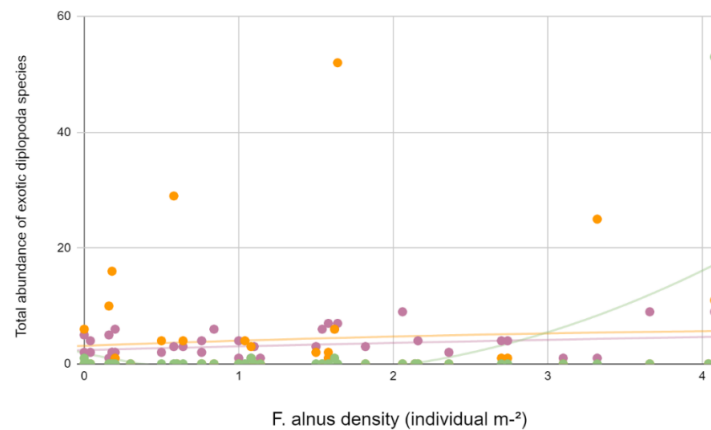
1.1.3 Summary statistics of RDA of understory plants

Summary statistics of redundancy analysis (RDA) of significant environmental variables (all standardized), *F. alnus* density (individual m⁻²), soil humidity (%), and tree canopy cover (%), associated with the cover (%) of understory plants species (Hellinger transformation) in communities following *F. alnus* density gradient between all the 43 plots in our study site, at L'Assomption.

Variable	Variance	F	Pr(>F)
<i>F. alnus</i> density	0.02269	2.0612	<0.05 *
Canopy cover (%)	0.03316	3.0123	<0.005**
Humidity (%)	0.03075	2.7931	<0.001***
Model	0.09656	2.1874	<0.001***
R²adjusted = 0,1038			

Note : Correlations were calculated for species structure based on ratio of the cover (to the closest 5%) of each species on total cover of native understory plant species.

1.1.4 Polynomial regression of exotic Diplopoda across the gradient of *F. alnus*



Polynomial regressions for total abundance of three exotic diplopoda species: *O. pilosus* (represented in red), *P. inconstans* (represented in orange) and *C. palmatus* (represented in green) across the density gradient of *F. alnus* across our study site. No statistically significant correlation is observed, but some tendencies are still showing with these species.

1.1.6 Summary statistics of RDA of macroarthropod communities

Summary statistics of redundancy analysis (RDA) of significant constraint variables (all standardized), *F. alnus* density (individual m⁻²), total native understory plant cover (%), native understory diversity (effective number of species), soil humidity (%), and woody debris cover (%), that are associated with specific variation in saprophagous macro arthropod communities (logarithmic transformation) between all the 43 sampling plots in study site, at L'Assomption.

Variable	Variance	F	Pr(>F)
<i>F. alnus</i> density (individual m ⁻²)	0.776	2.655	<0.05*
Native understory plant cover (%)	0.8095	2.9900	<0.005**
Effective number of plant species	0.377	1.289	<0.02*
Humidity (%)	1.5821	6.175	<0.001***
Woody debris cover(%)	0.752	2.571	<0.005**
Model	R²ajusted: 0.2287		< 0.001***

Note : Correlations were calculated for species structure based on ratio of average of the 3 saprophagous macro arthropod collects.

1.1.7 Diversity indices using litter composition as a predictive variable

Linear regressions models using *Frangula alnus* ratio in leaf litter and effective number of native understory plant species as predictive variables on different diversity index of saprophagous macroarthropods.

Dependent variable	Independent variable	Descriptive statistics		Linear models				R ²
		Mean ± SE	Median (Min-Max)	Estimate	SE	T-value	p-value	
Species richness ¹	<i>F. alnus</i> in leaf litter (%) Mean = 4.46 SE = 0.775	4.47 ± 0.13	5 (2-6)	-0.018	0.026	-0.686	0.497	0.011
Effective number of species		2.59 ± 0.11	2.49 (1.24-4.14)	-0.029	0.022	-1.317	0.195	0.041
Shannon-Wiener index (H')		0.91 ± 0.04	0.914 (0.26-1.42)	-0.011	0.009	-1.270	0.211	0.038
Evenness index (J')		0.60 ± 0.02	0.612 (0.216-0.881)	-0.007	0.005	-1.537	0.132	0.055
Total abundance ²		20.39 ± 1.8	20.3 (4.3-52.6)	-0.026	0.039	-0.670	0.507	0.011
Effective number of species	Effective number of plants species Mean= 7.07 SE = 0.3279	2.59 ± 0.11	2.49 (1.24-4.14)	0.07452	0.062	1.206	0.235	0.034
Total abundance ²		20.39 ± 1.8	20.3 (4.3-52.6)	0.02116	0.095	0.223	0.824	0.001

¹ Species richness' variation and effective number of species are very low (from 2 to 6 species), must be interpreted with caution.

² Square root transformation

1.1.8 Linear regression model excluding *T. rathkii*

Table of descriptive statistics and linear regression along density of *F. alnus* (individual m⁻²) as predictive variables on five community indices (species richness, effective number of species, Shannon-Wiener index, and evenness index) for saprophagous macroarthropod species excluding *T. rathkii*. Abundance of millipedes and woodlice have been transformed (square-root) to fit linear model conditions. All arthropod data are based on the total abundance of three collects within summer of 2020.

Dependent variable	Descriptive statistics		Linear model outputs				
	Mean ± SE	Median (Min-Max)	Estimate	Std error	T-value	Ajusted R ²	<i>p</i> -value
Species richness ¹	3.47 ± 0.13	4.00 (1.00-5.00)	0.2178	0.1104	1.972	0.064	0.0554.
Effective number of species	2.88 ± 2.15	2.82 (1.00-4.83)	-0.1900	0.1015	-1.872	0.0563	0.068.
Shannon-Wiener index (H') ²	0.99 ± 0.04	1.02 (0.00-1.57)	0.0909	0.0683	1.330	0.018	0.191
Evenness index (J')	0.81 ± 0.12	0.812 (0.46-1.00)	0.00385	0.01556	0.247	-0.023	0.806
Total abundance ³	18.16 ± 5.25	15.00 (3.00-64.00)	-0.1997	0.1943	-1.028	0.001	0.31

¹ Species richness' variation is very low (from 2 to 6 species), must be interpreted with caution.

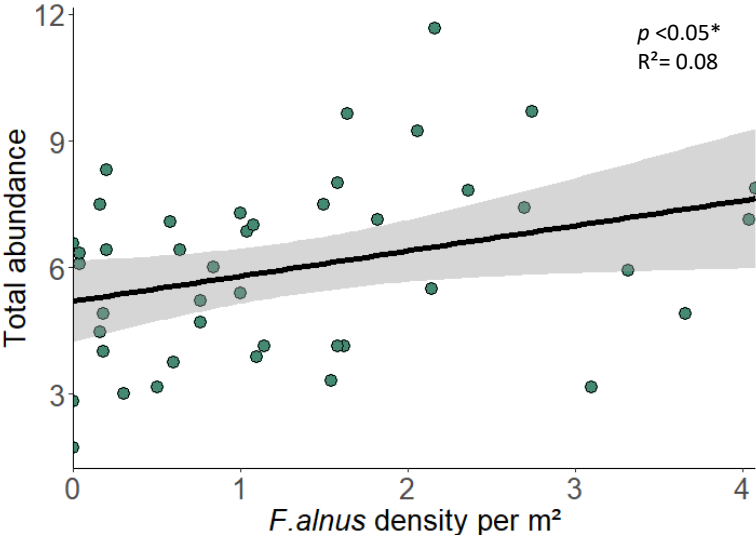
² Square transformed to fit linear regression model conditions.

³ Square root transformation to fit the linear regression model conditions.

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$

1.1.9 Linear regression model of *T. rathkii*

Linear regression model showing total abundance of squared abundance of *T. rathkii* along the *F. alnus* gradient of density. Most variation is not explained by explanatory variable ($R^2 = 0.08$), but still model still significant ($p = 0.0348$).



1.1.10 Other tested environmental explanatory variables

Other environmental variables were tested as explanatory variables on the effective number of species of native understory plant species and only leaf litter biomass showed to have an effect. Indeed, leaf litter biomass, which is composed of leaves of all plants and trees per plot, seems to negatively impact the understory plants' diversity in addition to *F. alnus* density ($R^2 = 0.2219$). Nevertheless, this output was not the primary focus of our research the explained variation percentage remains generally low, and no other measured environmental conditions expressed any relationship with the plant diversity indices. Moreover, in Table below, we observe that along the density gradient of *Frangula alnus*, not variation was observed in total leaf litter biomass. We therefore didn't investigate on these results as they seemed to be not relevant and not our primary focus.

Outputs of the tow most influential multiple linear models tested with most influential independent variables explaining variation in the effective number of native understory plant species This was based on AICc tests with *MuMin* package (Barton, 2020) on R program version 4.0.4 (R core Team 2021).

Multiple linear model outputs

Model's formula	Independent variables	Estimate	SE	T value	R ²	p-value
Effective number of species ~ F. alnus density + biomass litter	<i>F. alnus</i> density	-0.706767	0.255913	-2.762	0.2219	<0.01 **
	Litter biomass	-0.009453	0.004487	-2.107		<0.05 *
Effective number plants ~ F. alnus density + biomass litter + pH	<i>F. alnus</i> density	-0.807277	0.272835	-2.959	0.224	<0.01 **
	Litter biomass	-0.008940	0.004507	-1.984		0.054.
	Mean pH	-0.824501	0.783514	-1.052		0.153

CHAPITRE 3

DISCUSSION GÉNÉRALE

Les espèces végétales exotiques envahissantes sont connues depuis longtemps quant à leurs retombées négatives; au 17^e siècle, Pehr Kalm (envoyé par Carl Linné) les étudie scientifiquement pour la première fois et au 18^e siècle, Charles Darwin soulève une inquiétude quant à deux espèces de chardons européens dominant le paysage argentin (Simberloff, 2013). Les inquiétudes sur les EVEC ne datent donc pas d'hier et sont aujourd'hui grandement reconnues au sein des agences politiques, scientifiques et économiques (Kumar Rai & Singh, 2020; Lavoie, 2019). Dans le cadre de ce projet, l'étude menée sur l'espèce exotique envahissante *Frangula alnus* Miller soulève des impacts moins prononcés qu'attendus. Nos observations ont permis un discours plus atténué sur la sévérité des impacts de *Frangula alnus* sur la biodiversité et ont soulevé beaucoup d'enjeux sur l'incohérence et le manque de nuance retrouvé dans les connaissances générales associées aux EVEC.

3.1 RETOUR SUR LES POINTS SAILLANTS

F. alnus, pourrait posséder une meilleure capacité de cohabitation avec la flore indigène en comparaison avec d'autres EVEC (Aguilera et al., 2010; Kedzie-Webb et al., 2001). Il est également possible que l'envahissement par *F. alnus* sur notre site soit trop récent et qu'il n'ait pas atteint un seuil de densité critique pour observer des effets adverses (Panetta & Gooden, 2017). De plus, il est possible que le milieu étudié soit plus résistant à l'envahissement en fonction de ses conditions biotiques et abiotiques. Effectivement, il y avait une grande présence d'espèces végétales tolérantes à l'ombre, puisque l'échantillonnage a été réalisé dans un milieu boisé où l'accès à la lumière est limité par la canopée des arbres. Le couvert imposé par *F. alnus* serait donc moins prompt à affecter ces espèces, contrairement aux espèces des champs ou prairies, qui nécessitent beaucoup de lumière (Henry & Aarssen, 1997). Une différence d'effets en fonction du type d'habitat est également rapportée par Brousseau *et al.* (2021), où il y a un effet plus prononcé de *F. japonica* sur les plantes et les macro-arthropodes saprophages dans les prairies en comparaison aux forêts, potentiellement causé par une différence dans l'accumulation de la litière en milieux forestiers. De plus, les EVEC ont généralement une préférence pour les milieux ouverts et/ou perturbés (Lavoie, 2019). Il n'est donc pas surprenant que leurs effets sur les plantes basses dans les boisés soient moins rapportés et que les milieux ouverts soient généralement plus prompts à subir les effets néfastes des EVEC. Avec un gradient de densité de *F. alnus* seulement dans un seul type d'écosystème, nous n'avons pas eu l'occasion de comparer différents types milieux. Mais l'application de

cette méthodologie sur plusieurs milieux serait d'une grande pertinence pour de futures recherches. Cela permettrait la détermination d'un seuil associé à la sévérité de *F. alnus* et d'évaluer la résistance de différents milieux face à une invasion par celui-ci.

3.2 CONTROVERSES AVEC *FRANGULA ALNUS*

De nombreuses mentions dans la littérature grise et scientifique évoquent l'aspect néfaste de *F. alnus* pour la diversité des plantes basses indigènes. Ces propos sont également appuyés par plusieurs biologistes dans l'est de l'Amérique du Nord (Hamelin et al., 2016, 2017; Hébert & Thiffault, 2014; Lavoie, 2019; Schoeb et al., 2012). Pourtant, malgré l'augmentation importante de la densité et de la superficie de *F. alnus* (Aiello-Lammens, 2020; Catling & Porebski, 1994; Wingard, 2007), la littérature scientifique mettant en relation ses interactions avec la diversité végétale reste ambivalente et ne soulève pas forcément des effets négatifs (voir Annexe A). Dès lors, nous faisons face à deux discours encore bien en ébullition dans le monde scientifique, soulevés par Lavoie (2022) dans son ouvrage récemment publié : le premier étant *catastrophiste* rassemblant généralement toutes les EEE, et l'autre plus nuancé (quelquefois *invasosceptique*), issue des résultats équivoques des quelques études scientifiques.

La présomption que le *F. alnus* représente une grande menace pour les espèces végétales indigènes pourrait être expliquée par un manque de cohésion et une généralisation des impacts des EEEE à travers les multiples agences impliquées. Un bon exemple de ce phénomène peut s'observer dans les documents en ligne du *Global Invasive Species Database* (GISD), où l'information sur les impacts généraux de *F. alnus* n'est issue que d'articles scientifiques faisant surtout des associations indirectes des risques qui lui sont associés (GISD, 2005). Parmi ceux-ci, seulement l'article de Fagan et Peart (2004) investigate le lien direct entre la diversité et la présence de *F. alnus*. Les autres constituent surtout des études sur la biologie de *F. alnus* et de ses capacités d'envahissement (Catling & Porebski, 1994; Converse, 1984; Godwin, 1936; Godwin, 1943). De plus, il est pertinent de mentionner que la plupart des études ciblées par le GISD ont été publiées il y a plus de 25 ans (< 1995). Une revue de littérature comme celle-ci laisse présumer un réel manque de cohésion et d'actualisation entre les résultats observés en recherche scientifique et autres agences. Le GISD n'est seulement qu'un exemple parmi d'autres, car de nombreux autres documents font mention des risques associés à *F. alnus*, sans toutefois se référer à des sources crédibles (voir Annexe A).

Les discours contradictoires associés à *F. alnus* peuvent également être expliqués du fait qu'il soit souvent présenté avec une autre espèce de la même famille portant le même nom commun: *R. cathartica* (nerprun cathartique). Les deux arbustes ont longtemps été attribués au genre *Rhamnus*, mais cette classification a été discutée longuement pour finalement classer *F. alnus* dans le genre *Frangula* (Bolmgren & Oxelman, 2004; Gassmann et al., 2008). Toutefois, il arrive encore aujourd'hui que les deux nerpruns soient associés, principalement dans les documents gouvernementaux et de vulgarisation (Fig. 3.1). Sachant que les impacts négatifs de *R. cathartica* sur la biodiversité aient été bien documentés dans la littérature scientifique et soient moins équivoques que *F. alnus* (voir Annexe B), il est important d'être prudent avant de présumer un même degré de sévérité entre les EVEC.

3.3 CONTROVERSES GÉNÉRALES AVEC LES EVEC

La mise en évidence des incohérences associées à *F. alnus* a permis une réflexion plus large sur les controverses associées aux EVEC. En effet, malgré le consensus sur les risques associés aux EVEC, nous avons repéré quelques études scientifiques soulevant des impacts faibles ou inexistantes, autant pour *F. alnus* que d'autres EVEC (Diekmann et al., 2016; Jäger et al., 2009; Mills et al., 2009; Possessky et al., 2000; Ricciardi & Cohen, 2007; Rout & Callaway, 2009). Les multiples débats où la gravité à long terme des EVEC est soulevée sont d'ailleurs toujours d'actualité et soulignés par plusieurs auteurs et autrices (Lavoie, 2019, 2022). Pyšek *et al.*, (2012), dans leur méta-analyse, soulignent effectivement que 63,3% des études sur l'impact des EVEC rapportent des effets négatifs significatifs sur les communautés et les écosystèmes, laissant présumer un pourcentage considérable d'études avec des effets faibles ou sans effet. Cette grande variabilité à travers les conséquences



Figure 3.1 Feuilles et floraisons de *Frangula alnus* (image du haut), l'espèce étudiée dans le cadre de ce projet. Feuilles et floraisons de *Rhamnus cathartica* (image du bas), l'espèce végétale exotique envahissante souvent associée avec *F. alnus*. Source: Gabrielle Roberge

associées à l'envahissement soulève l'importance de cibler et hiérarchiser les espèces en fonction de leurs risques et du type de milieu envahi. Selon les différents contextes et variables, une même espèce pourrait avoir des effets bénéfiques, négatifs ou neutres en fonction des groupes étudiés et le type de milieu (Barney & Tekiela, 2020). Par exemple, une méta-analyse (Litt et al., 2014) a montré beaucoup de conséquences négatives chez certains groupes d'invertébrés causés par les EVEC, mais certaines EVEC, telles qu'*Agrostis capillaris* (agrostide commune) et *Anthoxanthum odoratum* (flouve odorante), sont associées à une augmentation d'abondance et de richesse chez les arthropodes édaphiques (Derraik et al., 2005). Litt et al. (2014) observent même que 67% des études sur les détritivores observent des effets bénéfiques des EVEC sur ce groupe faunique. Une autre méta-analyse (Nelson et al., 2017) indique que la majorité des études mettant en relation les EVEC et l'abondance des espèces aviaires ont des résultats neutres (57,2%) et que quelques-unes observent des effets négatifs (18,7%) et positifs (16,3%). Rout et Callaway (2009) soulèvent même un paradoxe associé aux EVEC, où souvent est observée une diminution de biodiversité, mais une augmentation de productivité (génération de biomasse).

Ces nuances ne sont pas étonnantes, puisque l'étude d'un écosystème demeure une opération très complexe et comporte une multitude de variables et d'échelles, en plus des nombreux facteurs pris en considération lors de la recherche. En effet, malgré la rigueur implicite dans la recherche scientifique, nous avons observé une absence de méthode uniforme lors de l'évaluation des risques associés aux EVEC, provoquant une littérature éclectique dans la sélection de variables, des unités de mesure et dans l'interprétation des résultats (Barney et al., 2013). En effet, certains-es chercheurs-es vont choisir le recouvrement foliaire (Mills et al., 2009), d'autres choisiront la densité (Burkle et al., 2012), l'aire basale des troncs (Frappier et al., 2003) ou simplement comparer une zone envahie à une zone non envahie (Diekmann et al., 2016). Plusieurs auteurs-ices ont même affirmé, il y a plusieurs années, que cette problématique ralentit les recherches en science prédictive sur les EVEC (Barney et al., 2013; Davis & Thompson, 2000). Caulotti et Richardson (2009) font également mention des incohérences présentes dans la sélection de variables et soulèvent qu'en absence de base ferme en écologie, n'importe quelle mesure d'impact peut être utilisée pour attribuer le titre « d'envahissant » à une espèce, rendant les généralisations difficiles ou inauthentiques.

3.4 GESTION ET INTERVENTION – LES IMPLICATIONS

Les différentes controverses soulignées précédemment, associées à complexité de la recherche en milieu naturel, rendent l'évaluation des impacts des EVEC très difficiles et peu efficient à utiliser pour la gestion en milieu pratique (Barney et al., 2013). En effet, ces incohérences et controverses au sein de la recherche

scientifique peuvent se perpétuer à travers les différentes agences impliquées dans la lutte aux espèces exotiques envahissantes (voir Annexe C). Ces nombreux enjeux compliquent la communication entre les différentes agences et inhibent considérablement l'élaboration de solutions ou de plans de gestion efficaces. Les groupes et organismes de conservation agissant auprès des EVEC possèdent rarement de bons outils pour guider leurs prises de décisions lors d'élaboration de plans d'intervention. Les plans de gestion sont donc souvent réalisés à partir d'une généralisation des problématiques et risques associés à aux EVEC, sans comparer le degré de sévérité associé entre les espèces. Par exemple, le plan d'intervention élaboré par Favreau-Leclerc et Levac (2019) est très adapté à la gestion de *R. cathartica* et inclus de nombreux critères à évaluer lors de la mise en place d'un plan d'action. Toutefois, l'espèce n'est jamais mise en relation avec d'autres EVEC et différents types de milieux envahis. Cette problématique a été rencontrée par plusieurs groupes de conservations. Par exemple, pour répondre à leurs contraintes budgétaires, le personnel de l'organisme CANOPÉE a été confronté à une sélection des EVEC à traiter dans les boisés urbains dont ils sont responsables. La mise en place d'un plan de gestion fut laborieuse pour l'équipe puisque les milieux étaient envahis par de multiples EVEC à caractéristiques très différentes, telles que *Phragmites australis* (roseau commun) et *R. cathartica* (Roberge, observation personnelle). Un autre groupe, L'Héritage Laurentien, a choisi d'intervenir auprès de *P. australis* et a renoncé à la gestion des autres EVEC sur certaines sections de leur site (D. Lynn, communication personnelle, 17 février 2022). Nous obtenons donc des d'interventions sans considération de la sévérité relative entre espèces, contraignant les gestionnaires à des choix arbitraires et économiques, plutôt qu'écologiques.

CONCLUSION

Nos résultats ont mis de l'avant que *F. alnus* a un effet négatif faible sur la diversité des plantes basses indigènes et négligeable sur les communautés des macro-arthropodes saprophages. Nos observations pourraient laisser sous-entendre qu'elles ne permettent pas de clarifier l'ambivalence retrouvée dans la littérature. Mais en complémentarité à la nature équivoque des autres études sur *F. alnus*, elles permettent d'atténuer le discours alarmiste et de souligner que cette espèce ne serait pas aussi problématique que d'autres EVEC, telles *R. cathartica* et *F. japonica*. Néanmoins, nous considérons que *F. alnus* représente certains risques pour la biodiversité locale et qu'il serait important de perpétuer les recherches sur ses impacts dans une plus grande variété de milieux.

Nous avons également remarqué un grand manque d'uniformité à travers les études scientifiques lors de l'évaluation des impacts des EVEC. Cette instabilité dans la recherche se répercute ensuite à travers les différentes agences impliquées et provoque des incohérences entre les discours scientifiques, gouvernementaux et des organismes gestionnaires. Ces problématiques nuisent considérablement à la lutte aux espèces exotiques envahissantes qui, selon l'IPBES (2019), est loin d'atteindre les objectifs établis par les *Sustainable Development Goals*. Pour atténuer les pertes associées à cet enjeu majeur, il sera impératif de viser une meilleure uniformisation au sein de la recherche scientifique, suggérée par Barney et Tekiela (2013). Dans le cadre d'un projet futur, cela permettrait également la création d'un outil d'aide à la gestion basé principalement sur une littérature scientifique uniformisée. Cet outil pourrait en effet comparer la sévérité des impacts associés aux différentes EVEC, en fonction des différents organismes ciblés, des types de milieux envahis, des coûts associés à leur gestion et des risques et pertes qu'elles engendrent.

En association avec les points précédents, nous proposons pour des projets futurs une hiérarchisation des EVEC dans les interventions en fonction de la sévérité de leurs impacts, ainsi qu'une meilleure définition des termes et une communication plus optimale entre les agences, afin de minimiser les problèmes associés à la gestion. Par l'entremise de nos observations et suggestions, nous pensons participer à la réduction de l'incohérence observée à travers ce sujet de grande ampleur. Malgré le travail colossal implicite, nous sommes fortement convaincus-es qu'une cohésion meilleure au sein de la recherche scientifique et entre les différentes instances optimisera l'utilisation des connaissances ainsi que la gestion pratique des EVEC.

ANNEXE A. RÉFÉRENCES DE LITTÉRATURE GRISE ET SCIENTIFIQUE SUR L'IMPACT DE *F. ALNUS* SUR LA DIVERSITÉ DES VÉGÉTAUX

Références de la littérature grise et scientifique (auteurs-ices) et année de publication répertoriées mettant en relation *Frangula alnus* sur la diversité et la composition des communautés végétales en Amérique du Nord. Les impacts sont déterminés dans le sens statistique du terme pour les publications scientifiques et soulevés lors de mention dans d'autres documents. Les caractères en gras mettent en évidence les résultats où *F. alnus* n'est pas problématique pour la diversité végétale

Auteurs-ices	Année de publication	Impacts
Articles scientifiques		
Reinartz et Klein**	1988	Dominant dans une tourbière et croissance logarithmique
Taft et Solecki **	1990	Dominant dans une tourbière
Possessky <i>et al.</i>	2000	Augmentation de la richesse des petits arbustes, aucun effet sur les herbacées. Dominance spécifique pour des espèces tolérantes à l'ombre
Frappier <i>et al.</i>	2003	Impact négatif sur densité de semis d'arbres et l'abondance et la richesse des plantes herbacées
Frappier <i>et al.</i>	2004	Impact négatif sur les petits arbres (non sur les herbacées)
Fagan et Peart	2004	Impact négatif sur la croissance et survie des jeunes arbres et favorise les espèces tolérantes à l'ombre
Houlahan et Findlay	2004	Augmentation de la richesse des végétaux indigènes
Mills <i>et al.</i>	2009	Aucun impact sur les plantes herbacées
Hamelin, Truax et Gagnon	2016	Réduction la survie et la croissance de deux espèces d'arbres (<i>Acer saccharinum</i> et <i>Quercus rubra</i>)
Hamelin, Truax et Gagnon	2017	Potentiel inhibition de croissances des plantations de 3 herbacées en présence de <i>F. alnus</i> . Mais statistiques non sign (p=0.097)
Publications non scientifiques ou livres *		
Shoeb, Truax et Gagnon	2012	Aucun impact observé
Hébert et Thiffault **	2014	Mention de diminution de la quantité de lumière pour les plantes basses et dominance.
Lavoie **	2019	Effet négatif sur les plantes basses, mais mention du manque d'études pour bien comprendre son impact.
Autres références *		

Global Invasive Species Database (GISD)	2005	Mention d'effets négatifs sur les semis d'arbres, rapporté par Frappier (2002), Fagan et Peart (2004) et Converse (1984). Les autres sources n'étudient pas les effets directs sur les végétaux indigènes de <i>F. alnus</i> et sont vieilles (<1995)
Marcil (Ville de Montréal)	2007	Mention que <i>F. alnus</i> compétitionne avec les espèces indigènes.
Michigan Dep. of Natural resources	2012	Mention que <i>F. alnus</i> compétitionne avec les espèces indigènes.
Anderson, H.	2012	Mention qu'il semble avoir un impact négatif sur les plantes basses, mais manque de sources scientifiques
Smallidge, Department of natural resources (NY)	2018	Mention que <i>F. alnus</i> réduit la régénération de la forêt et de la diversité des espèces végétales
Minnesota department of natural resources	NA	Mention que <i>F. alnus</i> compétitionne avec les autres espèces végétales pour les nutriments, la lumière et l'humidité.
Hebert, François	2019	Mention que <i>F. alnus</i> et <i>R. Cathartica</i> compétitionnent la régénération forestière
Nature Conservancy Canada (NCC)	2020	Mention que <i>F. alnus</i> compétitionne avec les plantes indigènes pour la lumière
Martel	2021	Mention des risques sur la biodiversité
Ontario invading species awareness program	2021	Mention des risques de <i>F. alnus</i> et <i>R. cathartica</i>
Memphrémagog MRC	NA	Mention que <i>F. alnus</i> et <i>R. cathartica</i> sont des nuisances pour les espèces indigènes

* Les articles gouvernementaux et de vulgarisation manquent de ressources scientifiques pour confirmer les impacts négatifs.

** Références qui n'étudient pas directement les impacts sur les plantes indigènes

ANNEXE B. TABLEAU COMPARATIF DE *F. ALNUS* ET *R. CATHARTICA* DANS LEURS IMPACTS SUR LES VÉGÉTAUX

Résumé du nombre de références comparant les deux espèces de nerpruns (*R. cathartica* et *F. alnus*) dans leurs impacts sur les végétaux dans les milieux envahis par ceux-ci. Pour les articles scientifiques, un impact négatif est déterminé par un résultat statistique significatif. Pour les articles de littérature grise tels les articles de vulgarisation, livres, documents gouvernementaux et autres références, nous avons sélectionné toutes les mentions impliquant un effet adverse sur la biodiversité végétale indigène (i.e., baisse de diversité, baisse d'abondance, menace pour espèces indigènes).

Espèce étudiée	Aucun impact	Impact négatif
Nerprun bourdaine (<i>Frangula alnus</i> Miller)		
Articles scientifiques	4	5
Articles de vulgarisation*	1	1
Livre	0	1
Documents gouvernementaux*	1	3
Autres références	0	2
Total :	6	12
Nerprun cathartique (<i>Rhamnus cathartica</i>)		
Articles scientifiques	0	9**
Articles de vulgarisation*	0	1
Livre	0	1
Documents Gouvernementaux*	0	3
Autres références	0	2
Total :	0	16

* Les articles gouvernementaux et de vulgarisation manquent de ressources scientifiques pour confirmer les impacts.

** deux articles inaccessibles (Leitner, 1986 et Alsum, 2012)

ANNEXE C. RÉFLEXIONS SUPPLÉMENTAIRES SUR LES INCOHÉRENCES

La gestion des espèces exotiques envahissantes comprend autant des enjeux scientifiques que politiques et pratiques. On retrouve en l'occurrence des groupes et organisation au niveau fédéral, provincial et municipal qui œuvrent dans ce domaine. Cette diversité d'agences apporte différentes terminologies et définitions qui peuvent être utilisée au sein de la problématique des EEE (Ricciardi & Cohen, 2007). Par exemple, le terme « envahissant » dans le domaine des sciences de l'écologie implique que l'espèce se propage rapidement, mais ne signifie pas implicitement qu'elle est une nuisance (Colautti et al., 2006; Ricciardi & Cohen, 2007). Mais pour les agences gouvernementales, il est implicite qu'une espèce envahissante cause des impacts négatifs pour les humains (Colautti et al., 2006; Gouvernement du Canada, 2004). La confusion dans les définitions cause un réel problème quant à l'interaction entre la science et les autres agences et porte à une généralisation globale des effets et des impacts associées aux différentes espèces. Ce problème a notamment été soulevé par Matthews *et al.* (2017), qui ont mentionné le manque de cohérence entre certains protocoles d'évaluation des risques associés aux EEE dans leur étude (six en Europe, un dans l'est de l'Amérique du Nord). Ils soulèvent entre-autre manque important d'uniformisation systémique dans la façon dont les impacts de chaque espèce sont évalués. Ce manque de nuance se reflète ensuite à travers les différents outils de communication entre les agences, provoquant ainsi des assumptions non basées sur les observations scientifiques. Ce problème a justement été observé avec notre espèce cible *Frangula alnus*, pour lequel nous avons trouvé un article journalistique lui attribuant le titre de « monstre sous surveillance » (Corriveau, 2016). Pourtant, malgré qu'il soit souvent présenté comme une espèce ayant des impacts sur la diversité des plantes indigènes, la littérature scientifique reste ambivalente sur ce sujet. Le manque de nuance, la variation dans la définition des termes et la généralisation quant aux EEEE causent des complications lors de l'élaboration de plans de gestions pour les contrôler (Barney & Tekiela, 2020).

BIBLIOGRAPHIE

- Aguilera, A. G., Alpert, P., Dukes, J. S., & Harrington, R. (2010). Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. *Biological Invasions*, 12(5), 1243-1252. <https://doi.org/https://doi.org/10.1007/s10530-009-9543-z>
- Aiello-Lammens, M. E. (2020). Observations of extended lag phase of nonnative invasive *Frangula alnus* (Rhamnaceae) may be spatial-scale dependent. *The Journal of the Torrey Botanical Society*, 147(2), 125-139. <https://doi.org/https://doi.org/10.3159/TORREY-D-17-00053.1>
- Anderson, H. (2012). *Invasive common (European) buckthorn (Rhamnus cathartica): Best management practices in Ontario*. Peterborough, ON: Ontario Invasive Plant Council Retrieved from https://www.ontarioinvasiveplants.ca/wpcontent/uploads/2016/06/OIPC_BMP_Buckthorn.pdf
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology letters* 9(6), 683-693. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- Archaux, F., Bergès, L., & Chevalier, R. (2007). Are plant censuses carried out on small quadrats more reliable than on larger ones? *Plant Ecology*, 188(2), 179-190.
- Bajcz, A. W. (2014). Reproductive ecophysiology of *Rubus occidentalis* in southeastern Michigan I. A survey of tolerance ranges. *Rhodora*, 116(967), 249-266.
- Barney, J. N., & Tekiel, D. R. (2020). Framing the concept of invasive species “impact” within a management context. *Invasive Plant Science and Management*, 13(2), 37-40. <https://doi.org/https://doi.org/10.1017/inp.2020.8>
- Barney, J. N., Tekiel, D. R., Dollete, E. S., & Tomasek, B. J. (2013). What is the “real” impact of invasive plant species? *Frontiers in Ecology and the Environment*, 11(6), 322-329. <https://doi.org/https://doi.org/10.1890/120120>
- Batzer, D. P., & Boix, D. (2018). *Invertebrates in freshwater wetlands*. Springer.
- Blair, J. M., Parmelee, R. W., & Wyman, R. (1994). A comparison of the forest floor invertebrate communities of four forest types in the northeastern US. *Pedobiologia*, 38, 146-146.
- Bolmgren, K., & Oxelman, B. (2004). Generic limits in *Rhamnus L. s.l.* (Rhamnaceae) inferred from nuclear and chloroplast DNA sequence phylogenies. *Taxon*, 53(2), 383-390.
- Borror, D., Triplehorn, C., & Johnson, N. (1992). Study of insects. In: Saunders College Publishing Harcourt Brace College Publishers.
- Avis Loi sur la conservation du patrimoine naturel (chapitre C-61.01), (2022).
- Braun-Blanquet, J. (1932). Pflanzensociologie Plant sociology. The study of plant communities.
- Braun-Blanquet, J. (1951). *Pflanzensociologie, grundzuge der vegetations kunde*.
- Brigić, A., Antonović, I., Alegro, A., Šegota, V., & Bujan, J. (2017). Terrestrial isopods (Isopoda: Oniscidea) as unexpected inhabitants of extreme habitats. *European Journal of Soil Biology*, 82, 66-71.
- Brouillet, L., Desmet, P., Coursol, F., Meades, S., Favreau, M., Anions, M., Bélisle, P., Gendreau, C., Shorthouse, D., & contributors. (2010). *Database of vascular plants of Canada (VASCAN)*.

- Brousseau, P.-M. (n.p.). *Clé d'identification des mille-pattes des milieux forestiers du Mont St-Bruno* [Identification Guide]. Université du Québec à Montréal.
- Brousseau, P.-M., Chauvat, M., De Almeida, T., & Forey, E. (2021). Invasive knotweed modifies predator-prey interactions in the soil food web. *Biological Invasions*, 23(6), 1987-2002. <https://doi.org/https://doi.org/10.1007/s10530-021-02485-9>
- Brousseau, P. M., Gravel, D., & Handa, I. T. (2018). On the development of a predictive functional trait approach for studying terrestrial arthropods. *Journal of Animal Ecology*, 87(5), 1209-1220. [https://doi.org/ https://doi.org/10.1111/1365-2656.12834](https://doi.org/https://doi.org/10.1111/1365-2656.12834)
- Brousseau, P. M., Gravel, D., & Handa, I. T. (2019). Traits of litter - dwelling forest arthropod predators and detritivores covary spatially with traits of their resources. *Ecology*, 100(10). <https://doi.org/https://doi.org/10.1002/ecy.2815>
- Brown, G. R., & Matthews, I. M. (2016). A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground - active arthropod biodiversity. *Ecology and Evolution*, 6(12), 3953-3964. [https://doi.org/ https://doi.org/10.1002/ece3.2176](https://doi.org/https://doi.org/10.1002/ece3.2176)
- Burkle, L. A., Mihaljevic, J. R., & Smith, K. G. (2012). Effects of an invasive plant transcend ecosystem boundaries through a dragonfly-mediated trophic pathway. *Oecologia*, 170(4), 1045-1052. <https://doi.org/https://doi.org/10.1007/s00442-012-2357-1>
- Butenschoen, O., Krashevskaya, V., Maraun, M., Marian, F., Sandmann, D., & Scheu, S. (2014). Litter mixture effects on decomposition in tropical montane rainforests vary strongly with time and turn negative at later stages of decay. *Soil Biology and Biochemistry*, 77, 121-128.
- Callaway, R. M., & Maron, J. L. (2006). What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology & Evolution*, 21(7), 369-374. <https://doi.org/10.1016/j.tree.2006.04.008>
- Callaway, R. M., & Ridenour, W. M. (2004). Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, 2(8), 436-443. [https://doi.org/https://doi.org/10.1890/1540-9295\(2004\)002\[0436:NWISAT\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2)
- Canadian Food Inspection Agency. (2008). *Invasive Alien plants in Canada*. Ottawa, ON: CFIA
- Cárcamo, H. A., Abe, T. A., Prescott, C. E., Holl, F. B., & Chanway, C. P. (2000). Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. *Canadian Journal of Forest Research*, 30(5), 817-826.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., & Wardle, D. A. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59-67.
- Catling, P. M., & Porebski, Z. S. (1994). The history of invasion and current status of glossy buckthorn, *Rhamnus frangula*, in southern Ontario. *Canadian field-naturalist. Ottawa ON*, 108(3), 305-310.
- Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., & Hobbie, S. E. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234-242. <https://doi.org/https://doi.org/10.1038/35012241>
- Colautti, R. I., Bailey, S. A., Van Overdijk, C. D., Amundsen, K., & MacIsaac, H. J. (2006). Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, 8(1), 45-59.
- Converse, C. K. (1984). Element stewardship abstract for *Rhamnus cathartica*, *Rhamnus frangula* (syn. *Frangula alnus*). *The Nature Conservancy: Arlington, VA, USA*.

- Corriveau, A. (2016). Le nerprun bourdaine, un monstre sous surveillance à Magog. <https://ici.radio-canada.ca/nouvelle/783818/nerprun-envahissant-marais-cerises-magog-granby>
- Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., Mundepi, A., Phillips, C. A., & Callaham, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, 110, 116-133. <https://doi.org/10.1016/j.soilbio.2017.03.008>
- CPTAQ. (1996). *Décision*. (60027 - 240463). Commission de protection du territoire agricole du Québec, à L'Assomption
- David, J. F., & Handa, I. T. (2010). The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biological Reviews - Cambridge* 85(4), 881-895. <https://doi.org/10.1111/j.1469-185X.2010.00138.x>
- Davis, M. A., & Thompson, K. (2000). Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the ecological society of America*, 81(3), 226-230. <https://www.jstor.org/stable/20168448>
- De Kort, H., Mergeay, J., Jacquemyn, H., & Honnay, O. (2016). Transatlantic invasion routes and adaptive potential in North American populations of the invasive glossy buckthorn, *Frangula alnus*. *Annals of Botany*, 118(6), 1089-1099. <https://doi.org/https://doi.org/10.1093/aob/mcw157>
- De Oliveira, T., Hättenschwiler, S., & Tanya Handa, I. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, 24(4), 937-946.
- Delanoy, L., & Archibold, O. (2007). Efficacy of control measures for European buckthorn (*Rhamnus cathartica* L.) in Saskatchewan. *Environmental management*, 40(4), 709-718. <https://doi.org/https://doi.org/10.1007/s00267-006-0409-1>
- Derraik, J. G. B., Rufaut, C. G., Closs, G. P., & Derraik, K. J. M. D. (2005). Ground invertebrate fauna associated with native shrubs and exotic pasture in a modified rural landscape, Otago, New Zealand. *New Zealand journal of ecology*, 29(1), 129-136.
- Diekmann, M., Effertz, H., Baranowski, M., & Dupré, C. (2016). Weak effects on plant diversity of two invasive *Impatiens* species. *Plant Ecology*, 217(12), 1503-1514. <https://doi.org/https://doi.org/10.1007/s11258-016-0663-0>
- Duelli, P., Obrist, M. K., & Schmatz, D. R. (1999). Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture ecosystems and environment* 74(1-3), 33-64. [https://doi.org/https://doi.org/10.1016/S0167-8809\(99\)00029-8](https://doi.org/https://doi.org/10.1016/S0167-8809(99)00029-8)
- Ehrenfeld, J. G. (2003). Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems*, 6(6), 503-523. <https://doi.org/https://doi.org/10.1007/s10021-002-0151-3>
- EnvironnementCanada. (2021). *Historical Data*. Gouvernement du Canada Retrieved from https://climate.weather.gc.ca/historical_data/search_historic_data_e.html
- Fagan, M., & Peart, D. (2004). Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *Forest Ecology and Management*, 194(1-3), 95-107. <https://doi.org/https://doi.org/10.1016/j.foreco.2004.02.015>
- Favreau-Leclerc, A. (2019). *Prévention et contrôle du nerprun cathartique au Québec* [Université de Sherbrooke].

- Fiedler, A. K., Landis, D. A., & Arduser, M. (2012). Rapid Shift in Pollinator Communities Following Invasive Species Removal. *Restoration Ecology*, 20(5), 593-602. <https://doi.org/10.1111/j.1526-100X.2011.00820.x>
- Frappier, B., Eckert, R. T., & Lee, T. D. (2003). Potention impacts of the invasive exotic shrub Rhamnus Frangula (Glossy Buckthorn) on forest of Southern New Hampshire. *Northeastern Naturalist*, 10(3), 277-296. [https://doi.org/https://doi.org/10.1656/1092-6194\(2003\)010\[0277:PIOTIE\]2.0.CO;2](https://doi.org/https://doi.org/10.1656/1092-6194(2003)010[0277:PIOTIE]2.0.CO;2)
- Frappier, B., Eckert, R. T., & Lee, T. D. (2004). Experimental Removal of the Non-indigenous Shrub Rhamnus frangula (Glossy Buckthorn): Effects on Native Herbs and Woody Seedlings. *Northeastern Naturalist* 11(3), 313-322. [https://doi.org/https://doi.org/10.1656/1092-6194\(2004\)011\[0333:EROTNS\]2.0.CO;2](https://doi.org/https://doi.org/10.1656/1092-6194(2004)011[0333:EROTNS]2.0.CO;2)
- Gabillot, C., Meyer, J., Manka, F., Raymond-Léonard, L.-J. H., T., & Kneeshaw, D. (2019). *Le nerprun au Boisé des terres noires*.
- Garcia-Tejero, S., & Taboada, A. (2016). Microhabitat heterogeneity promotes soil fertility and ground-dwelling arthropod diversity in Mediterranean wood-pastures. *Agriculture, Ecosystems and Environment*, 233, 192-201. <https://doi.org/https://doi.org/10.1016/j.agee.2016.09.004>
- Gassmann, A., Tosevski, I., & Skinner, L. (2008). Use of native range surveys to determine the potential host range of arthropod herbivores for biological control of two related weed species, Rhamnus cathartica and Frangula alnus. *Biological Control*, 45(1).
- Gerber, E., Krebs, C., Murrell, C., Schaffner, U., Moretti, M., & Rocklin, R. (2008). Exotic invasive knotweeds (Fallopia spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation*, 141(3), 646-654. <https://doi.org/https://doi.org/10.1016/j.biocon.2007.12.009>
- Gerlach, J., Samways, M., & Pryke, J. (2013). Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*, 17(4), 831-850.
- GISD. (2005). *Full account for : Frangula alus* <http://www.iucngisd.org/gisd/speciesname/Frangula+alnus>
- Godwin, H. (1936). Studies in the ecology of wicken fen: III. The establishment and development of fen scrub (carr). *The Journal of Ecology*, 82-116.
- Godwin, H. (1943). Frangula Alnus Miller. *Journal of Ecology*, 31(1), 77-92.
- Gooden, B., & French, K. (2014). Non - interactive effects of plant invasion and landscape modification on native communities. *Diversity and distributions*, 20(6), 626-639. <https://doi.org/https://doi.org/10.1111/ddi.12178>
- Gouvernement du Canada. (2004). *Stratégie nationale sur les espèces exotiques envahissantes* Retrieved from https://publications.gc.ca/collections/collection_2014/ec/CW66-394-2004-fra.pdf
- Hamelin, C., Gagnon, D., & Truax, B. (2016). Invasive glossy buckthorn impedes growth of red oak and sugar maple under-planted in a mature hybrid poplar plantation. *New Forests*, 47(6), 897-911.
- Hamelin, C., Gagnon, D., & Truax, B. (2017). Exotic Invasive Shrub Glossy Buckthorn Reduces Restoration Potential for Native Forest Herbs. *Sustainability*, 9(2), 249. <https://doi.org/https://doi.org/10.3390/su9020249>
- Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M. O., Jabiol, J., & Makkonen, M. (2014). Consequences of biodiversity loss for litter decomposition

- across biomes. *Nature*, 509(7499), 218-221.
<https://doi.org/https://doi.org/10.1038/nature13247>
- Hébert, F., & Thiffault, N. (2014). Le nerprun bourdaine: un envahisseur exotique qui menace l'établissement des plantations. *Canadian Field-Naturalist*, 108, 305-310.
- Heimpel, G. E., Frelich, L. E., Landis, D. A., Hopper, K. R., Hoelmer, K. A., Sezen, Z., Asplen, M. K., & Wu, K. (2010). European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. *Biological Invasions*, 12(9), 2913-2931.
- Hejda, M., Pyšek, P., & Jarošík, V. c. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, 97(3), 393-403. <https://doi.org/https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Heneghan, L., Clay, C., & Brundage, C. (2002). Rapid Decomposition of Buckthorn Litter May Change Soil Nutrient Levels. *Ecological Restoration*, 20(2), 108-111. <https://www.jstor.org/stable/43442545>
- Heneghan, L., Rauschenberg, C., Fatemi, F., & Workman, M. (2004). European Buckthorn (*Rhamnus cathartica*) and its Effects on Some Ecosystem Properties in an Urban Woodland. *Ecological Restoration*, 22(4). <https://www.jstor.org/stable/43442776>
- Henry, H. A., & Aarssen, L. W. (1997). On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos*, 575-582.
- Higman, P. C. S. (2009). *A Field Identification Guide to Invasive Plants in Michigan's Natural Communities*. Michigan: Michigan State University Extension
- Hopkin, S. P., & Read, H. J. (1992). *Biology of millipedes*. Oxford University Press.
- Houlahan, J. E., & Findlay, C. S. (2004). Effect of Invasive Plant Species on Temperate Wetland Plant Diversity. *Journal of the Torrey Botanical Society*, 18(4), 1132-1138. <https://doi.org/https://doi.org/10.1111/j.1523-1739.2004.00391.x>
- Humbert, L. (2006). Tolérance et largeur de niche des espèces herbacées des forêts québécoises vis-à-vis du PH et de la lumière.
- IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services*. Zenodo.
- IPBES. (2020). The IPBES global assessment: Pathways to action. *Trends in Ecology & Evolution*, 35(5), 407-414.
- IPCC. (2022). *Climate change 2022: impacts, adaptation and vulnerability (AR6)*. C. U. Press.
- Jäger, H., Kowarik, I., & Tye, A. (2009). Destruction without extinction: long-term impacts of an invasive tree species on Galápagos highland vegetation. *Journal of Ecology*, 97(6), 1252-1263. [https://doi.org/ https://doi.org/10.1111/j.1365-2745.2009.01578.x](https://doi.org/https://doi.org/10.1111/j.1365-2745.2009.01578.x)
- Jass, J., & Klausmeier, B. (2000). Endemics and Immigrants: North American Terrestrial Isopods (Isopoda, Oniscidea) North of Mexico. *Crustaceana*, 73(7), 771-799. <https://doi.org/https://doi.org/10.1163/156854000504804>
- Jędrzykowski, W. B. (1982). Millipedes (Diplopoda) of Warsaw and Mazovia. *Memorabilia Zoologica*; 36, 36, 253-261. <https://rcin.org.pl/miiz/publication/28318>
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113(2), 363-375. <https://doi.org/https://doi.org/10.1111/j.2006.0030-1299.14714.x>

- Kaul, A. D., & Wilsey, B. J. (2021). Exotic species drive patterns of plant species diversity in 93 restored tallgrass prairies. *Ecological Applications*, 31(2). <https://doi.org/https://doi.org/10.1002/eap.2252>
- Kedzie-Webb, S. A., Sheley, R. L., Borkowski, J. J., & Jacobs, J. S. (2001). Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist*, 43-49. <https://www.jstor.org/stable/41717075>
- Klionsky, S. M., Amatangelo, K. L., & Waller, D. M. (2011). Above - and belowground impacts of European buckthorn (*Rhamnus cathartica*) on four native forbs. *Restoration Ecology*, 19(6), 728-737. <https://doi.org/https://doi.org/10.1111/j.1526-100X.2010.00727.x>
- Kumar Rai, P., & Singh, J. S. (2020). Invasive alien plant species: Their impact on environment, ecosystem services and human health. *Ecological Indicators*, 111. <https://doi.org/https://doi.org/10.1016/j.ecolind.2019.106020>
- Lalk, S., Hartshorn, J., & Coyle, D. R. (2021). Invasive Woody Plants and Their Effects on Arthropods in the United States: Challenges and Opportunities. *Annals of the Entomological Society of America*, 114(2), 192-205. <https://doi.org/https://doi.org/10.1093/aesa/saaa054>
- Langor, D. W., deWaard, J. R., & Snyder, B. A. (2019). Myriapoda of Canada. *ZooKeys*(819), 169. <https://doi.org/10.3897/zookeys.819.29447>
- Lavoie, C. (2019). *50 plantes envahissantes: protéger la nature et l'agriculture*. Les Publications du Québec.
- Lavoie, C. (2022). *40 autres plantes envahissantes*.
- Lavoie, C., Guay, G. v., & Joerin, F. (2014). Une Liste des Plantes Vasculaires Exotiques Nuisibles du Québec : Nouvelle Approche Pour la Sélection Des Espèces et L'aide à la Décision. *Ecoscience*, 21(2), 133-156. <https://doi.org/10.2980/21-2-3703>
- Leboeuf, M. (2016). *Arbres et plantes forestières du Québec et des maritimes—Réédition*. Éditions Michel Quintin.
- Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271-280. <https://doi.org/https://doi.org/10.1007/s004420100716>
- Litt, A. R., Cord, E. E., Fulbright, T. E., & Schuster, G. L. (2014). Effects of Invasive Plants on Arthropods. *Conservation Biology*, 28(6), 1532-1549. <https://doi.org/https://doi.org/10.1111/cobi.12350>
- Lowry, E., Rollinson, E. J., Laybourn, A. J., Scott, T. E., Aiello-Lammens, M. E., Gray, S. M., Mickley, J., & Gurevitch, J. (2013). Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution*, 3(1), 182-196. <https://doi.org/https://doi.org/10.1002/ece3.431>
- Magura, T., Hornung, E., & Tóthmérész, B. (2008). Abundance patterns of terrestrial isopods along an urbanization gradient. *Community Ecology*, 9(1), 115-120. <https://doi.org/https://doi.org/10.1556/comec.9.2008.1.13>
- Marie-Victorin, F. (1995). Flore laurentienne. 3e édition mise à jour par L. Brouillet, SG Hay et I. Goulet en collaboration avec M. Blondeau, J. Cayouette et J. Labrecque édition. Les Presses de l'Université de Montréal, Montréal.
- Martel, M.-J. (2021). *Guide de gestion du nerprun bourdaine pour les propriétaires forestiers*. Cookshire-Eaton: Agence de mise en valeur de la forêt privée de l'Estrie.

- Matthews, J., van der Velde, G., Collas, F. P., de Hoop, L., Koopman, K. R., Hendriks, A. J., & Leuven, R. S. (2017). Inconsistencies in the risk classification of alien species and implications for risk assessment in the European Union. *Ecosphere*, 8(6), e01832. <https://doi.org/https://doi.org/10.1002/ecs2.1832>
- McCary, M. A., Mores, R., Farfan, M. A., & Wise, D. H. (2016). Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: A meta - analysis. *Ecology letters* 19(3), 328-335. <https://doi.org/https://doi.org/10.1111/ele.12562>
- McLeod, M. L., Cleveland, C. C., Lekberg, Y., Maron, J. L., Philippot, L., Bru, D., & Callaway, R. M. (2016). Exotic invasive plants increase productivity, abundance of ammonia - oxidizing bacteria and nitrogen availability in intermountain grasslands. *Journal of Ecology*, 104(4), 994-1002. <https://doi.org/https://doi.org/10.1111/1365-2745.12584>
- Michigan Department of Natural Resources. (2012). *Glossy buckthorn*. Michigan: Michigan Natural Features Inventory
- Mills, J. E., Reinartz, J. A., Meyer, G. A., & Young, E. B. (2009). Exotic shrub invasion in an undisturbed wetland has little community-level effect over a 15-year period. *Biological invasions* 11(8), 1803-1820. <https://doi.org/https://doi.org/10.1007/s10530-008-9359-2>
- Mitchell, M. G. E., Bennett, E. M., & Gonzalez, A. (2014). Agricultural landscape structure affects arthropod diversity and arthropod-derived ecosystem services. *Agriculture, Ecosystems & Environment*, 192.
- Moizuk, G. A., & Livingston, R. B. (1966). Ecology of red maple (*Acer rubrum* L.) in a Massachusetts upland bog. *Ecology*, 47(6), 942-950.
- Molano-Flores, B. (2014). An invasive plant species decreases native plant reproductive success. *Natural Areas Journal*, 34(4), 465-469.
- Moore, J. C., Berlow, E. L., Coleman, D. C., de Ruiter, P. C., Dong, Q., Hastings, A., Johnson, N. C., McCann, K. S., Melville, K., & Morin, P. J. (2004). Detritus, trophic dynamics and biodiversity. *Ecology letters* 7(7), 584-600. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2004.00606.x>
- Nelson, S. B., Coon, J. J., Duchardt, C. J., Kranz, A. J., Parker, C. M., Swartz, T. M., Miller, J. R., Fischer, J. D., Halsey, S. J., & Schneider, S. C. (2017). Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biological Invasions*, 19(5), 1547-1563. <https://doi.org/10.1007/s10530-017-1377-5>
- National environmental policy act of 1969, 8-32 (1970) Yannacone Jr, Victor J.
- Noël, F., & Séchet, E. (2007). Crustacés Isopodes terrestres du Nord-Ouest de la France (Crustacea, Isopoda, Oniscidea). *Invertébrés Armoricains*, 2, 1-48.
- O'Neill, R. V. (1968). Population Energies of the Millipede, *Narceus Americanus* (Beauvois). *Ecology*, 49(5), 804-809.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community ecology package*, 10(631-637), 719.
- Olson, L. J. (2006). The economics of terrestrial invasive species: a review of the literature. *Agricultural and Resource Economics Review*, 35(1), 178-194.
- Panetta, F. D., & Gooden, B. (2017). Managing for biodiversity: impact and action thresholds for invasive plants in natural ecosystems.

- Pansu, M., & Gautheyrou, J. (2006). *Handbook of soil analysis : mineralogical, organic and inorganic methods*. Springer. <https://doi.org/10.1007/978-3-540-31211-6>
- Paoletti, M. G., & Hassall, M. (1999). Woodlice (Isopoda: Oniscidea): their potential for assessing sustainability and use as bioindicators. *Agriculture, Ecosystems & Environment*, 74(1-3), 157-165.
- Pellerin, S., Mercure, M., Desaulniers, A., & Lavoie, C. (2009). Changes in plant communities over three decades on two disturbed bogs in southeastern Québec. *Applied Vegetation Science*, 12(1), 107-118.
- Peterson, C. J., & Pickett, S. T. (1995). Forest reorganization: a case study in an old - growth forest catastrophic blowdown. *Ecology*, 76(3), 763-774.
- Petrulaitis, L., & Gudžinskas, Z. (2020). The first records of two alien woody species, *Cornus alternifolia* and *Cornus amomum*, in Lithuania. *Bioinvasions records*, 9(2), 384-392.
- PFAF. (2022). *Galeopsis ladanum* - L. <https://pfaf.org/user/Plant.aspx?LatinName=Galeopsis+ladanum>
- Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, 50(1), 53-65.
- Pisula, N. L., & Meiners, S. J. (2010). Relative allelopathic potential of invasive plant species in a young disturbed woodland. *The Journal of the Torrey Botanical Society*, 137(1), 81-87. <https://doi.org/https://doi.org/10.3159/09-RA-040.1>
- Possessky, S. L., Williams, C. E., & Moriarity, W. J. (2000). Glossy buckthorn, *Rhamnus frangula* L.: A threat to riparian plant communities of the northern Allegheny Plateau (USA). *Natural Areas Journal*, 20(3), 290-292. <https://www.jstor.org/stable/43911925>
- Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, 18(5), 1725-1737. <https://doi.org/> <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- Qureshi, H., Anwar, T., Habib, N., Ali, Q., Haider, M. Z., Yasmin, S., Munazir, M., Basit, Z., & Waseem, M. (2021). Multiple comparisons of diversity indices invaded by *Lantana camara*. *Brazilian journal of biology = Revista brasleira de biologia*, 81(1), 83-91. <https://doi.org/10.1590/1519-6984.222147>
- Reinartz, J. A., & Kline, J. (1988). Glossy buckthorn (*Rhamnus frangula*), a threat to the vegetation of the Cedarburg Bog.
- Ricciardi, A., & Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, 9(3), 309-315. <https://doi.org/https://doi.org/10.1007/s10530-006-9034-4>
- Richmond, C. E., Breitburg, D. L., & Rose, K. A. (2005). The role of environmental generalist species in ecosystem function. *Ecological modelling*, 188(2-4), 279-295. <https://doi.org/https://doi.org/10.1016/j.ecolmodel.2005.03.002>
- Robertson, M. P., Harris, K. R., Coetzee, J. A., Foxcroft, L. C., Dippenaar-Schoeman, A. S., & van Rensburg, B. J. (2011). Assessing local scale impacts of *Opuntia stricta* (Cactaceae) invasion on beetle and spider diversity in Kruger National Park, South Africa. *African Zoology*, 46(2), 205-223. <https://doi.org/https://doi.org/10.1080/15627020.2011.11407496>
- Roiloa, S. R., Yu, F.-H., & Barreiro, R. (2020). Plant invasions: Mechanisms, impacts and management. In (Vol. 267, pp. 151603): Elsevier.

- Roth, A. M., Whitfeld, T. J., Lodge, A. G., Eisenhauer, N., Frelich, L. E., & Reich, P. B. (2015). Invasive earthworms interact with abiotic conditions to influence the invasion of common buckthorn (*Rhamnus cathartica*). *Oecologia*, *178*(1), 219-230.
- Rout, M. E., & Callaway, R. M. (2009). An Invasive Plant Paradox. *Science*, *324*(5928), 734-735. <https://doi.org/10.1126/science.1173651>
- Sabu, T. K., Shiju, R. T., Vinod, K. V., & Nithya, S. (2011). A Comparison of the Pitfall Trap, Winkler Extractor and Berlese Funnel for Sampling Ground-Dwelling Arthropods in Tropical Montane Cloud Forests. *Journal of Insect Science*, *11*(28), 1-19. <https://doi.org/https://doi.org/10.1673/031.011.0128>
- Salamon, J. A., Wissuwa, J., Jagos, S., Koblmuller, M., Ozinger, O., Winkler, C., & Frank, T. (2011). Plant species effects on soil macrofauna density in grassy arable fallows of different age. *European Journal of Soil Biology*, *47*(2), 129-137. <https://doi.org/10.1016/j.ejsobi.2011.01.004>
- Sanford, G. R., Jackson, R. D., Booth, E. G., Hedtcke, J. L., & Picasso, V. (2021). Perenniality and diversity drive output stability and resilience in a 26-year cropping systems experiment. *Field Crops Research*, *263*, 108071.
- Schirmel, J., Lenze, S., Katzmann, D., & Buchholz, S. (2010). Capture efficiency of pitfall traps is highly affected by sampling interval. *Entomologia Experimentalis et Applicata*, *136*(2), 206-210.
- Schoeb, J., Truax, B., & Gagnon, D. (2012). Le nerprun bourdaine, un envahisseur à la conquête des forêts du sud du Québec. *Le Progrès Forestier*, 8-12.
- Schuh, M., & Larsen, K. J. (2015). *Rhamnus cathartica* (Rosales: Rhamnaceae) Invasion Reduces Ground-Dwelling Insect Abundance and Diversity in Northeast Iowa Forests. *Environmental entomology* *44*(3), 647-657. <https://doi.org/https://doi.org/10.1093/ee/nvv050>
- Shakir, M. M., & Ahmed, S. (2015). Seasonal abundance of soil arthropods in relation to meteorological and edaphic factors in the agroecosystems of Faisalabad, Punjab, Pakistan. *International Journal of Biometeorology*, *59*(5), 605-616. <https://doi.org/10.1007/s00484-014-0874-9>
- Shelley, R. (1988). The millipeds of eastern Canada (Arthropoda: Diplopoda). *Canadian Journal of Zoology*, *66*(7), 1638-1663.
- Shelley, R. (2002). The millipeds of central Canada (Arthropoda: Diplopoda), with reviews of the Canadian fauna and diplopod faunistic studies. *Canadian Journal of Zoology*, *80*, 1863-1875. <https://doi.org/https://doi.org/10.1139/z02-170>
- Shrestha, U. B., Sharma, K. P., Devkota, A., Siwakoti, M., & Shrestha, B. B. (2018). Potential impact of climate change on the distribution of six invasive alien plants in Nepal. *Ecological Indicators*, *95*, 99-107. <https://doi.org/https://doi.org/10.1016/j.ecolind.2018.07.009>
- Shultz, J. W. (2018). A guide to the identification of the terrestrial Isopoda of Maryland, USA (Crustacea). *ZooKeys*(801), 207. <https://doi.org/10.3897/zookeys.801.24146>
- Siemann, E. (1998). Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, *79*(6), 2057-2070. [https://doi.org/https://doi.org/10.1890/0012-9658\(1998\)079\[2057:ETOEOP\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(1998)079[2057:ETOEOP]2.0.CO;2)
- Sierwald, P., Hennen, D. A., Zahnle, X. J., Ware, S., & Marek, P. E. (2019). Taxonomic synthesis of the eastern North American millipede genus *Pseudopolydesmus* (Diplopoda: Polydesmida: Polydesmidae), utilizing high-detail ultraviolet fluorescence imaging. *Zoological Journal of the Linnean Society*, *187*(1), 117-142. <https://doi.org/10.1093/zoolinnean/zlz020>

- Simberloff, D. (2013). *Invasive species: what everyone needs to know*. Oxford University Press.
- Southwood, T. R., Brown, V., & Reader, P. (1979). The relationships of plant and insect diversities in succession. *Biological journal of the Linnean society*, 12(4), 327-348.
<https://doi.org/https://doi.org/10.1111/j.1095-8312.1979.tb00063.x>
- Stanton, K. M., Weeks, S. S., Dana, M. N., & Mickelbart, M. V. (2010). Light exposure and shade effects on growth, flowering, and leaf morphology of *Spiraea alba* Du Roi and *Spiraea tomentosa* L. *HortScience*, 45(12), 1912-1916.
- Stokdyk, J. P., & Herrman, K. S. (2014). Short-Term Impacts of *Frangula alnus* Litter on Forest Soil Properties. *Water, Air, & Soil Pollution*, 225(6). <https://doi.org/10.1007/s11270-014-2000-3>
- Stokdyk, J. P., & Herrman, K. S. (2016). Effects of *Frangula alnus* on soil microbial communities and biogeochemical processes in Wisconsin forests. *Plant and Soil*, 409(1), 65-75.
<https://doi.org/https://doi.org/10.1007/s11104-016-2916-z>
- Taft, J. B., & Solecki, M. K. (1990). Vascular flora of the wetland and prairie communities of Gavin Bog and Prairie Nature Preserve, Lake County, Illinois. *Rhodora*, 142-165.
- Tilman, D. (2000). Causes, consequences and ethics of biodiversity. *Nature*, 405(6783), 208-211.
<https://doi.org/https://doi.org/10.1038/35012217>
- Topping, C. J., & Sunderland, K. D. (1992). Limitations to the Use of Pitfall Traps in Ecological Studies Exemplified by a Study of Spiders in a Field of Winter Wheat. *Journal of Applied Ecology*, 29(2), 485-491. <https://doi.org/https://doi.org/10.2307/2404516>
- USDA. (n.p.). United States Department of Agriculture. <https://plants.usda.gov/home>
- van Gestel, C. A., & Loureiro, S. (2018). Terrestrial isopods as model organisms in soil ecotoxicology: a review. *ZooKeys*(801), 127. <https://doi.org/10.3897/zookeys.801.21970>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta - analysis of their effects on species, communities and ecosystems. *Ecology letters* 14(7), 702-708. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., & Westbrooks, R. (1996). Biological invasions as global environmental change. *American Scientist* <https://pubag.nal.usda.gov/catalog/61>
- Vivanco, J. M., Bais, H. P., Stermitz, F. R., Thelen, G. C., & Callaway, R. M. (2004). Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. *Ecology letters* 7(4), 285-292.
- Vyn, R. (2019). *Estimated expenditures on invasive species in Ontario: 2019 Survey Results* (Report. Invasive Species Centre. Sault St. Marie, ON, Issue.
- Warren, R. J., Labatore, A., & Candeias, M. (2017). Allelopathic invasive tree (*Rhamnus cathartica*) alters native plant communities. *Plant Ecology*, 218(10), 1233-1241.
- WeatherSpark. (2021). *Daily Precipitation in the Summer of 2020 at L'Assomption*.
<https://weatherspark.com/h/s/147212/2020/1/Historical-Weather-Summer-2020-at-L'Assomption-Canada#Figures-PrecipitationProbability>
- Wenk, E. S., Callahan, M. A., O'Brien, J. J., & Hanson, P. J. (2016). Soil Macroinvertebrate Communities Across a Productivity Gradient in Deciduous Forests of Eastern North America. *Northeastern Naturalist*, 23(1), 25-44. <https://doi.org/10.1656/045.023.0103>

- Wingard, H. S. (2007). *Invasion of transition hardwood forests by exotic Rhamnus frangula: Chronology and site requirements*. University of New Hampshire.
- Yates, E. D., Levia Jr, D. F., & Williams, C. L. (2004). Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. *Forest Ecology and Management*, 190(2-3), 119-130. <https://doi.org/https://doi.org/10.1016/j.foreco.2003.11.008>
- Zeleny, D. (2021). *Analysis of community ecology data in R*. https://www.davidzeleny.net/anadat-r/doku.php/en:rda_cca