UNIVERSITÉ DU QUÉBEC EN OUTAOUAIS

IMPORTANCE DES FRÊNES POUR LA BIODIVERSITÉ DANS LES FORÊTS RIPARIENNES SOUS INFLUENCE DU CASTOR (*Castor canadensis*) ET DE L'AGRILE DU FRÊNE (*Agrilus planipennis*).

THÈSE

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AVANT-PROPOS

Cette thèse de doctorat est constituée de trois chapitres, dont chacun fait l'objet d'un article scientifique. Pour ces trois chapitres, j'ai déterminé les objectifs de recherche, réalisé les analyses statistiques et rédigé les articles, sans toutefois négliger l'importance qu'a pu jouer ma direction dans la mise en place de ce projet. Ils ont en effet participé activement à la réalisation de ces trois chapitres, et leurs commentaires ont contribué à l'amélioration de ceux-ci.

Le premier chapitre de cette thèse a été publié dans le journal *Forests* en octobre 2022 pour lequel mon directeur, le Dr. François Lorenzetti, et ma co-directrice, la Dr Angélique Dupuch sont les seuls coauteurs.

Le deuxième chapitre de cette thèse a été soumis à *Journal of mammalogy* en mai 2023, et pour cet article également, mon directeur, le Dr. François Lorenzetti, et ma co-directrice, la Dr Angélique Dupuch sont les seuls coauteurs.

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RÉSUMÉ

Avec l’invasion de l’agrile du frêne (*Agrilus planipennis*) en Amérique du Nord, les frênes (*Fraxinus* spp.) sont fortement menacés, et la grande majorité de ceux-ci sont voués à disparaitre dans les années à venir. En forêt tempérée décidue, les frênes peuvent être un genre dominant des forêts ripariennes. Ces forêts sont considérées comme des zones écologiques très importantes, puisqu’elles constituent l’interface entre deux milieux et qu’elles jouent de nombreux rôles écologiques. Elles sont par ailleurs connues pour abriter une biodiversité animale et végétale importante. La disparition subite d’un genre qui peut être dominant dans ce type de forêt a donc le potentiel d’agir significativement sur la biodiversité de ce milieu, et les fonctions écosystémiques qui en découlent. On sait aussi que les frênes sont des essences qui peuvent être appréciées par le castor (*Castor canadensis*), un rongeur qui influence considérablement la structure des écosystèmes ripariens. Par leur sélection alimentaire, les castors peuvent en effet façonner la composition forestière, en favorisant les essences qu’ils évitent et en défavorisant les essences qu’ils sélectionnent. Le rôle charnière que les frênes pourraient jouer dans la dynamique des colonies de castors et dans le maintien d’une biodiversité particulière au sein des forêts ripariennes n’a pas fait l’objet d’études spécifiques. La disparition du frêne a aussi le potentiel d’affecter les communautés d’invertébrés, non seulement par la modification subite de la structure de la forêt, mais aussi par la disparition de la litière de frêne qui est connue pour sa labilité, ce qui pourrait faire diminuer la vitesse de décomposition de la litière dans les forêts ripariennes. Cette question n’a pas non plus encore fait l’objet d’études spécifiques : dans la littérature, les études semblent se focaliser principalement sur les effets de la modification structurelle de la forêt, et sur certaines familles d’invertébrés uniquement. Pour tenter de répondre à ces différentes questions, nous avons effectué trois études distinctes au parc national de Plaisance, qui seront présentées sous forme de trois chapitres dans ce doctorat.

Le premier chapitre de ce doctorat vise à évaluer la place exacte des frênes dans le régime alimentaire du castor, et à déterminer comment le comportement alimentaire du castor pourrait être modifié par leur disparition. Il a pu être démontré que le frêne était bien la ressource alimentaire la plus importante pour les castors parmi celles disponibles. En effet, seules deux autres essences (le charme, *Carpinus* spp. et le peuplier, *Populus* spp.) avaient plus de probabilité d’être consommées

que les frênes, mais leur faible abondance dans le parc ne leur permettait pas d'être considérées comme les ressources alimentaires les plus importantes. Nous avons également pu démontrer que les gaules de charmes pourraient voir leur probabilité de consommation augmenter avec la disparition des frênes matures. Par ailleurs, si les gaules de frênes diminuaient en abondance, ou disparaissaient, il est possible que la probabilité de consommation des érables matures, des gaules de tilleuls et de charmes puisse diminuer. Cependant, ce dernier effet pourrait, en réalité, être dû à un cas de compétition apparente.

Le deuxième chapitre de ce doctorat avait pour but de déterminer si la disparition des frênes avait la capacité de diminuer les densités de population de castor. Ce mammifère étant une espèce sociale et territoriale, ses densités de population peuvent être régulées par la taille du groupe, la taille du territoire, ou les deux. Nous avons pu mettre en évidence que la densité des frênes sur les territoires influençait positivement la taille du groupe, mais pas la taille du territoire, ce qui est surprenant pour une espèce aussi territoriale. La disparition des frênes est donc susceptible de faire décroitre les populations de castors dans les forêts ripariennes dominées par cette essence.

Finalement, dans le troisième chapitre, nous avions comme premier objectif de déterminer si le frêne était bien l'essence qui influençait positivement la labilité dans une litière composée majoritairement de frêne et d'érable (*Acer* spp.). Deuxièmement, nous voulions déterminer si en plus des effets de la modification de la structure forestière qui sont connus, la modification de la litière avait la capacité d'influencer les communautés d'invertébrés. Nous avons pu déterminer que la vitesse de décomposition de la litière était effectivement en grande partie déterminée par le pourcentage de frênes dans celle-ci. Par ailleurs, nous avons pu montrer que les frênes, probablement par leur litière, influençaient les communautés d'invertébrés : les assemblages de familles étaient différents suivant la proportion de frênes dans la canopée, démontrant que certaines communautés associées aux frênes sont singulières. Enfin, certaines familles avaient une diversité taxinomique influencée positivement pas la vitesse de décomposition de la litière, ce qui implique que la disparition des frênes pourrait avoir des effets négatifs sur la biodiversité à l'échelle des forêts ripariennes.

L'ensemble de la thèse a permis d'établir que la disparition des frênes va très probablement diminuer la densité de population de castors et modifier leur comportement alimentaire, ce qui

entraînera des conséquences sur la dynamique forestière. Par ailleurs, si les frênes étaient remplacés par des arbres ayant une litière moins labile, cela pourrait très certainement affecter négativement la biodiversité des invertébrés du sol. Bien qu'il ne soit pas possible de déterminer précisément à quoi ressembleront les forêts ripariennes du futur, ce doctorat aura permis de mettre en évidence que dans les forêts où il est abondant, le frêne constitue une espèce clé de voûte tant pour la biodiversité animale que pour la composition forestière, par l'entremise de son effet sur les castors.

Mots-clés : Agrile du frêne, Frêne, Forêts ripariennes, Castor d'Amérique, Invertébrés, Forêt tempérée, Perturbation

ABSTRACT

With the invasion of North America by the emerald ash borer (*Agrilus planipennis*), ash trees (*Fraxinus* spp.) are under severe threat and the vast majority are destined to disappear in the coming years. In temperate deciduous forests, ash can be a dominant genus of riparian forests. These forests are considered to be very important ecological zones, as they form the interface between two ecosystems and play numerous ecological roles. They are also known to harbour significant plant and animal biodiversity. The sudden disappearance of a genus that may be dominant in this type of forest therefore has the potential to significantly impact the biodiversity of this type of environment and the ecosystem services that derive from it. We also know that ash is a genus that can be appreciated by beavers (*Castor canadensis*), which have a considerable influence on the structure of riparian ecosystems. Through their food selection, beavers can in fact shape forest composition, favoring species they avoid and disfavoring species they select. The pivotal role that ash trees could play in the dynamics of beaver colonies and in the maintenance of a particular biodiversity within riparian forests has not been the subject of specific studies. The disappearance of ash trees also has the potential to impact invertebrate communities, not only through a sudden change in forest structure, but also through the disappearance of ash litter, kmown for its lability, which could reduce the decomposition rate of the remaining litter. This question has not yet been the subject of specific studies either: in the literature, studies seem to focus mainly on the effects of structural modification of the forest, and only on certain families of invertebrates. To answer these questions, we carried out three separate studies in Parc national de Plaisance, which will be presented in three chapters of this thesis.

The first chapter of this thesis will aim to assess the exact place of ash in the beaver's diet, and how the beaver's feeding behaviour might be altered by the disappearance of ash. It has been shown that ash is indeed the most important food resource for beavers among those tested. In fact, only two other species (musclewood, *Carpinus* spp., and poplar, *Populus* spp.) were more likely to be consumed than ash, but their low abundance in the park meant that they could not be considered the most important food resource. We were also able to demonstrate that musclewood saplings could see their probability of consumption increase with the disappearance of mature ash trees. On the other hand, if the abundance of the ash saplings decreased, it is possible that the probability of consumption of mature maple, basswood and musclewood saplings could decrease. However, this latter effect could be due to a case of apparent competition.

The aim of the second chapter of this thesis was to determine whether the disappearance of ash have the capacity to reduce the densities of the beaver population. Being a social and territorial species, the population densities may be regulated by group size, territory size, or both. We were able to show that the density of ash in the territories positively influenced the size of the group, but had no effect on the territory size, which is surprising for such a territorial species. The disappearance of ash is therefore likely to reduce beaver populations in riparian forests dominated by this genus.

Finally, in the third chapter, our first objective was to determine whether ash was indeed the genus that positively influenced lability in a litter composed mainly of ash and maple (*Acer* spp.). Secondly, we wanted to determine whether, in addition to the effects of altered forest structure, altered litter had the capacity to influence invertebrate communities. We were able to determine that the rate of litter decomposition was, indeed, largely determined by the percentage of ash in the litter. We were also able to show that ash, probably through its litter, influences invertebrate communities: the family assemblages were different depending on the proportion of ash trees in the canopy, demonstrating that some ash-associated communities are singular. Finally, some families had a taxonomic diversity positively influenced by litter decomposition rate, implying that the disappearance of ash could have negative effects on biodiversity at the scale of riparian forests.

Taken together, these chapters show that the disappearance of ash trees will most likely reduce beaver population density and alter their feeding behaviour, with consequent effects on forest dynamics. Furthermore, if ash trees were replaced by trees with less labile litter, this could certainly have a negative impact on the biodiversity of soil invertebrates. Although it is not possible to precisely determine what the riparian forests of the future will look like, this thesis will have shown that in temperate forests where ash is abundant, it is a keystone for both animal biodiversity and forest composition, through its effect on beavers.

Keywords: Emerald ash borer, Ash, Riparian forests, American beaver, Invertebrates, Temperate Forest, Disturbance

INTRODUCTION

1.1 Contexte général

Les perturbations naturelles sont des évènements généralement soudains qui vont venir modifier l'écosystème selon une intensité et une fréquence pouvant varier suivant les perturbations et les écosystèmes. Un grand nombre d'évènements peuvent être considérés comme des perturbations naturelles. Certains de ces évènements sont abiotiques, comme les incendies, le vent, les crues (Crandall *et al.*, 2003; Krebs *et al.*, 2010; Mitchell, 2013), et d'autres sont biotiques comme les ravages liés aux insectes (Przepióra *et al.*, 2020). Ces perturbations peuvent être nécessaires au bon fonctionnement de l'écosystème, en jouant des rôles écologiques majeurs. En effet, des perturbations intenses comme les régimes d'incendies peuvent favoriser la biodiversité des forêts en permettant aux communautés de coexister, qu'il s'agisse des communautés animales ou végétales (Kelly *et al.*, 2017; Thom & Seidl, 2016). Les rôles écologiques des feux sont même beaucoup plus larges, et incluent notamment la modification de la composition chimique des sols, ou la germination de certaines espèces d'arbres, favorisant la succession forestière (Ahlgren & Ahlgren, 1960). Il est cependant important de noter que les rôles bénéfiques des feux relèvent des régimes naturels, et que le réchauffement climatique, en augmentant la fréquence et l'intensité de ces perturbations dans certaines régions, cause des effets néfastes sur l'environnement, car la capacité de résilience de celui-ci est dépassée (Halofsky *et al.*, 2020; Johnstone *et al.*, 2010). D'autres perturbations, moins intenses, peuvent favoriser elles aussi certains taxons en augmentant leur abondance, comme c'est le cas avec les inondations annuelles dans les forêts ripariennes (Lambeets *et al.*, 2008). Les maladies et les ravages des insectes impactant les forêts peuvent également être des perturbations régulières. En Amérique du Nord par exemple, des insectes comme la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*, Clemens), ou la livrée des forêts (*Malacosoma disstria*, Hübner) sont des espèces dont les cycles réguliers provoquent des dégâts parfois importants aux peuplements (Boulanger *et al.*, 2012; Gross, 1991; Moulinier *et al.*, 2011; Spence & Maclean, 2011), mais font partie d'une dynamique naturelle en place, puisqu'elles sont régulées par des facteurs environnementaux, comme le parasitisme, la prédation et l'abondance des ressources (Royama, 1984; Smith & Goyer, 1986). Malgré les dommages importants qu'ils causent aux forêts, les insectes font tout de même partie du régime normal de perturbations et peuvent, eux aussi, augmenter la biodiversité (Beudert *et al.*, 2015; Thom & Seidl, 2016).

En revanche, certaines perturbations biotiques peuvent avoir un effet bien plus délétère, car elles n'entrent pas dans le régime naturel des forêts. C'est le cas des espèces exotiques envahissantes qui ne peuvent bien souvent pas être régulées. En Amérique du Nord, la graphiose de l'orme (ou maladie hollandaise de l'orme) est un parfait exemple de cette problématique. Cette maladie a été introduite dans les années 1930 par l'intermédiaire d'un insecte exotique : le scolyte européen (*Scolytus multistriatus,* Marsh). Les scolytes sont les vecteurs de dispersion des champignons (*Ophiostoma ulmi,* Buisman et *Ophiostoma novo-ulmi,* Brasier) responsables de la maladie (Karnosky, 1979). Cette maladie a tué des millions d'ormes (principalement *Ulmus Americana,* Linnaeus) en Amérique du Nord, et a été responsable d'une catastrophe écologique (Karnosky, 1979), modifiant profondément la canopée et la litière des forêts infestées (Marks, 2017).

Beaucoup plus récemment, l'invasion en Amérique du Nord par un insecte exotique envahissant a également causé une grande perturbation dans plusieurs habitats : l'agrile du frêne (*Agrilus planipennis* Fairmaire). L'arrivée de l'agrile du frêne est relativement récente au Canada, avec le premier rapport officiel de cette espèce en 2002 (Haack *et al.*, 2002). Dans les zones où il est présent, l'agrile entraîne la mortalité de plus de 99% des frênes quelques années seulement après l'invasion des peuplements (Klooster *et al.*, 2014), ce qui pourrait à moyen terme mener à la disparition presque complète des espèces de ce genre au Canada. Les derniers rapports montrent que l'agrile a été détecté jusqu'en Gaspésie en 2023 (canada.ca), démontrant que sa répartition approche les limites de l'aire de répartition du frêne noir et du frêne d'Amérique (Figure 0.1, Hope *et al.*, 2021). La mortalité des frênes induite par l'agrile entraine des modifications dans les forêts, à la fois par la diminution de l'apport de feuilles dans la litière, et par la création de trouées dans la canopée (Nisbet *et al.*, 2015). Cette mortalité a aussi des effets en cascade, à la fois directs et indirects, sur les processus écosystémiques et les interactions écologiques. En effet, la litière est modifiée par la disparition des frênes, notamment au niveau des cycles de l'azote et du carbone (Kolka *et al.,* 2018). De plus, la création de trouées dans la canopée engendre à la fois l'augmentation de la luminosité et de la température, et corollairement, la diminution de l'humidité du sol (Gálhidy *et al.*, 2006). Ces trouées et l'accumulation de bois mort pourraient à leur tour causer une altération des cycles biogéochimiques et des interactions écologiques en modifiant la structure et les conditions de l'habitat.

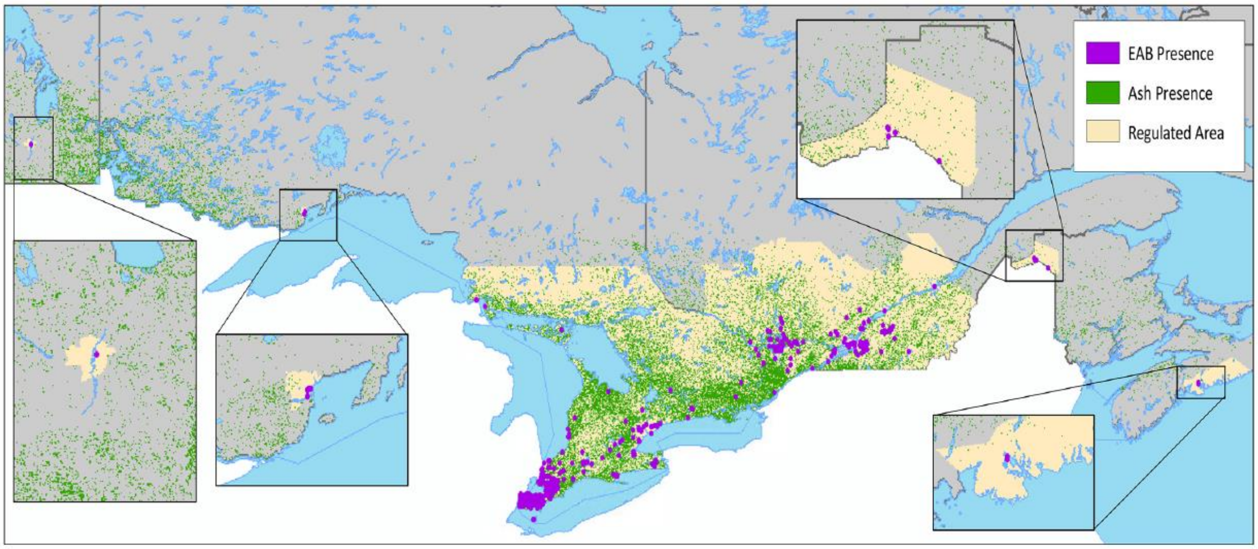

Figure 0.1 : Carte issue de Hope *et al.*, (2021) représentant la présence de frênes (vert) et les présences détectées de l'agrile du frêne (violet) dans l'est du Canada selon les données de 2019 de l'Agence canadienne d'inspection des aliments

Dans l'est de l'Amérique du Nord, notamment dans le sud du Québec, les frênes (*Fraxinus* spp.) sont des essences relativement fréquentes des forêts ripariennes, en particulier le frêne noir (*F. nigra*) qui est connu pour être tolérant aux conditions hydriques du sol de ces forêts (Engelken & McCullough, 2020). Les forêts ripariennes sont les bandes forestières situées en bordure des cours d'eau, qui sont inondées pendant les crues printanières, puis exondées pendant l'été. Elles possèdent généralement une végétation particulière, qui va rechercher, ou tolérer de telles conditions hydriques (Rousseau, 1962). Ces forêts constituent l'interface entre le milieu aquatique et le milieu terrestre, faisant de celles-ci des écotones (Nisbet *et al.*, 2015). En dépit de leur superficie restreinte, les forêts en zone riparienne ont des fonctions écologiques majeures et variées (Ewel *et al.*, 2001), comme entre autres la rétention des sédiments (Vigiak *et al.*, 2016), la régulation des crues (Cooper *et al.*, 2021), la stabilisation des rives (Abernethy & Rutherfurd, 2000), la filtration de divers polluants (Lowrance, 2000) et les flux de nutriments (Vought *et al.*, 1994). La production végétale de ces milieux permet de soutenir les invertébrés non seulement terrestres, mais aussi aquatiques, car elles constituent des apports allochtones de matière organique (Polis *et al.*, 1997; Swan & Palmer, 2006) qui constitueront la base des réseaux trophiques de ces deux milieux (Collier *et al.*, 2002; Murakami & Nakano, 2001; Ramey & Richardson, 2017; Wipfli, 1997). Enfin, ces bandes forestières sont connues pour abriter une biodiversité faunique et floristique particulièrement riche (Forio *et al.*, 2020; Gagnon & Gangbazo, 2007; Maisonneuve & Rioux, 2001; Paine & Ribic, 2002). Pour l'ensemble de ces raisons, ces forêts sont cruciales pour l'environnement, et leur conservation constitue un enjeu majeur (Hunter *et al.*, 2017). Déterminer l'impact de la disparition d'un genre pouvant être dominant dans ces forêts s'avère donc nécessaire pour évaluer si leur intégrité écologique sera conservée. Avec la présence de l'agrile du frêne s'esquisse un patron au niveau des forêts ripariennes qui n'est pas sans rappeler la diminution importante dans ces milieux de l'orme d'Amérique par la graphiose de l'orme. Ce parallèle est d'autant plus marqué que l'orme et le frêne ont des qualités écologiques similaires (Marks, 2017), notamment au niveau de la litière forestière qu'elles génèrent (Schindler & Gessner, 2009). Les frênes ont la particularité de produire une litière assez labile, c'est-à-dire dont le taux de décomposition est élevé (Palik *et al.*, 2005). Les études comparant la vitesse de décomposition du frêne à d'autres essences montrent d'ailleurs que celle du frêne fait généralement partie des vitesses parmi les plus élevées (Palik *et al.*, 2005; Petersen *et al.*, 1974). Une plus grande vitesse de décomposition peut être favorable à la biodiversité animale, car elle génère un habitat propice aux invertébrés, en fournissant rapidement une quantité importante de ressources alimentaires (Palik *et al.*, 2005).

1.2 Les invertébrés du sol

La disparition du frêne, qui va profondément changer les forêts ripariennes, est également susceptible de fortement affecter les communautés d'invertébrés du sol en modifiant leur habitat et la quantité de ressources disponible, ce qui aura probablement des retombées importantes sur toute la biodiversité animale occupant ces forêts, mais pourrait également entraîner des conséquences encore plus profondes.

1.2.1 Importance des invertébrés du sol

Les invertébrés du sol jouent un rôle majeur dans les forêts ripariennes. D'une part, ils constituent bien souvent la base des réseaux trophiques. Certains groupes d'invertébrés, notamment les décomposeurs, sont des consommateurs primaires qui vont se nourrir des feuilles et des racines des arbres (Hättenschwiler *et al.*, 2005; Pollierer *et al.*, 2007). D'autres invertébrés sont considérés comme des consommateurs secondaires, puisque se nourrissant de différents taxons d'invertébrés (Mogi, 2007). Enfin, les invertébrés du sol seront consommés par différentes espèces de vertébrés, qu'elles soient terrestres ou aquatiques et qui sont à la base de la chaine trophique (Collier *et al.*, 2002; Murakami & Nakano, 2001; Ramey & Richardson, 2017; Wipfli, 1997). D'autre part, certains taxons d'invertébrés du sol jouent un rôle majeur dans la structuration et la composition du sol, et dans divers fonctions et services écosystémiques comme les lombrics et les collemboles, qui vont entre autres, augmenter la teneur en azote du sol, participer à la décomposition de la litière, et soutenir la production primaire en favorisant la croissance de certaines plantes (Jouquet *et al.*, 2006; Partsch *et al.*, 2006; Sharma *et al.*, 2017). Déterminer si la disparition des frênes a le potentiel de modifier la composition des communautés d'invertébrés de manière durable est donc très important pour caractériser et quantifier l'amplitude des bouleversements que l'agrile du frêne pourra entrainer.

1.2.2 Modifications de la forêt riparienne

La modification du milieu engendrée par l'agrile devrait entrainer des changements dans la biodiversité faunique (Gandhi & Herms, 2010a). À court et moyen terme, les communautés d'invertébrés seront modifiées, au moins partiellement, par les changements structurels de la forêt riparienne. En effet, la mort des frênes entrainera des trouées dans la canopée (Gandhi *et al.*, 2014; Ulyshen *et al.*, 2011), une augmentation de la quantité de bois mort (Perry, Herms, *et al.*, 2018), et une augmentation du couvert de plantes herbacées (Engelken *et al.*, 2020) liée à l'ouverture de la canopée. Tous ces facteurs sont susceptibles d'avoir un effet sur la biodiversité des invertébrés, par exemple en augmentant l'abondance relative de certaines espèces, ce qui modifiera par le fait même les communautés d'invertébrés (Černecká *et al.*, 2020; Gandhi *et al.*, 2014; Grodsky *et al.*, 2018a; Perry, Wallin, *et al.*, 2018; Perry & Herms, 2016a). Cependant, ces effets devraient tous être amenés à diminuer avec le temps, parce que ces trouées se résorberont progressivement à mesure que d'autres arbres les coloniseront, et que le bois mort se décomposera. Ce dernier point pourrait prendre plusieurs décennies, bien que le frêne soit connu pour avoir une vitesse de décomposition élevée (Aulen *et al.*, 2012; Harmon & Sexton, 1996; Lasota *et al.*, 2022; Perry, Herms, *et al.*, 2018).

Cependant, l'invasion de l'agrile pourrait avoir le potentiel d'affecter les communautés d'invertébrés sur le long terme, voire de manière permanente, selon les essences qui remplaceront le frêne. Si les essences de remplacement ont des propriétés et une vitesse de décomposition différente de celle du frêne, il est en effet possible que les modifications que subiront les communautés d'invertébrés soient définitives. Pour ces raisons, il est donc important de mieux caractériser comment les différentes modifications engendrées par l'agrile du frêne affecteront les communautés d'invertébrés, car les effets de la modification structurelle et des modifications de la litière ne sont pas encore connus.

Cette invasion biologique pourrait également entrainer dans les forêts ripariennes des modifications drastiques dans le comportement d'un ingénieur de l'écosystème qui a la capacité de façonner la composition forestière : le castor (*Castor canadensis* Kuhl). Cela pourrait modifier d'autant plus les dynamiques forestières existantes, modifiant la biodiversité végétale, et entrainant par le fait même des potentielles rétroactions qui pourraient avoir une incidence sur la biodiversité animale.

1.3 Le castor

La biodiversité végétale des forêts ripariennes est en grande partie déterminée par cette espèce de mammifère semi-aquatique répandue à travers toute l'Amérique du Nord. En effet, étant l'interface entre le milieu aquatique et le milieu terrestre, les forêts ripariennes sont très largement utilisées par les castors qui y trouvent à la fois leur nourriture et leurs matériaux de construction (Collen & Gibson, 2001). Le castor est une espèce ingénieure qui joue un rôle clé en raison de l'impact important qu'elle peut avoir sur l'écosystème dans lequel elle se trouve. Il façonne et crée de nouveaux écosystèmes grâce à la construction de barrages, permettant la création de retenues d'eau (Naiman *et al.*, 1986; Rosell *et al.*, 2005). Cependant, la création de barrages et les inondations qu'il peut provoquer ne sont pas ses seuls rôles dans l'écosystème. Son régime alimentaire, notamment constitué d'arbres et de gaules, fait de lui un acteur influençant la succession forestière, mais aussi la composition des peuplements (Donkor & Fryxell, 2000; Johnston & Naiman, 1990). Ainsi, en abattant de manière sélective les arbres, le castor modifie la dynamique et le couvert forestier en favorisant les espèces qu'il évite, et en défavorisant les espèces qu'il sélectionne (Barnes & Dibble, 1988).

1.3.1 Alimentation

1.3.1.1 Sélection alimentaire

Le castor est souvent qualifié de généraliste sélectif « *choosy generalist* » (Vorel *et al.*, 2015). Il a la capacité de s'alimenter sur l'ensemble des essences présentes dans son environnement, mais exhibera de fortes préférences pour certaines d'entre elles. La préférence du castor pour les essences au sein des forêts ripariennes semble dépendante du contexte (essences présentes, dimensions des tiges, distances à la hutte ou à la rive) (Fryxell & Doucet, 1993; Raffel *et al.*, 2009). Ses essences préférées sont généralement les saules (*Salix spp.*), les chênes (*Quercus spp.*), les peupliers (*Populus spp.*) et les frênes (*Fraxinus spp.*) (Gallant *et al.*, 2004; Gerwing *et al.*, 2013; Müller-Schwarze *et al.*, 1994; Raffel *et al.*, 2009). En effet, dans les forêts ripariennes en biome tempéré, les frênes peuvent être abondants et sont parfois rapportés comme l'essence la plus appréciée par le castor (Barnes & Dibble, 1988). Cette préférence pour les frênes peut encore évoquer le parallèle avec l'orme d'Amérique, qui faisait également partie des essences les plus appréciées par le castor (Marks, 2017). Enfin, lorsque leurs essences favorites sont en faible densité, les castors sont rapportés comme devenant moins sélectifs, et vont généralement consommer les essences les plus abondantes, afin de minimiser leur temps de recherche et maximiser leur gain d'énergie (Gallant *et al.*, 2004; Hood & Bayley, 2009). Si le frêne est effectivement l'une des essences favorites du castor, on peut postuler que sa disparition pourrait entrainer une modification dans la sélection alimentaire du castor. Cependant, il reste indispensable de tester si la sélection du frêne qui a été observée dans certaines études l'est aussi dans l'écosystème à l'étude, car celui-ci n'a pas encore fait l'objet d'études spécifiques.

1.3.1.2 Comportement alimentaire

La connaissance approfondie du comportement d'alimentation du castor pourrait s'avérer très utile pour déterminer l'avenir de la forêt en zone riparienne, car le taux de consommation de chaque essence par le castor pourrait dépendre de sa disponibilité. En effet, on sait que le taux de consommation d'une ressource est dépendant de sa disponibilité; cette réponse du taux de consommation vis-à-vis de la disponibilité est appelée réponse fonctionnelle, et peut prendre trois formes (Holling, 1959). La réponse fonctionnelle de type I correspond à une relation linéaire entre le nombre de proies consommées et leur densité. La réponse fonctionnelle de type II est caractérisée par un taux de consommation décroissant à mesure que la densité de proies augmente. La réponse fonctionnelle de type III est caractérisée par un taux de consommation croissant à faible densité, avant d'atteindre un maximum et de devenir décroissant (Holling, 1959). Dans la littérature, le castor est rapporté comme ayant une réponse fonctionnelle de type II (Fryxell *et al.*, 1994), qui est très commune chez les mammifères herbivores, bien qu'une réponse de type III ait été également mentionnée (Fryxell & Doucet, 1993). En effet, un point d'inflexion sur la courbe de consommation pourrait indiquer une relation stabilisante pour les densités des espèces favorites (Fryxell & Doucet, 1993). Dans une telle situation, il y aurait un effet stabilisant à long terme sur la disponibilité de la ressource (Hammill *et al.*, 2010; Holling, 1959; Sarnelle & Wilson, 2008) car le pourcentage de tiges consommées diminuerait en dessous d'une certaine densité de ressources, contrairement à la réponse fonctionnelle de type II (Figure 0.1).

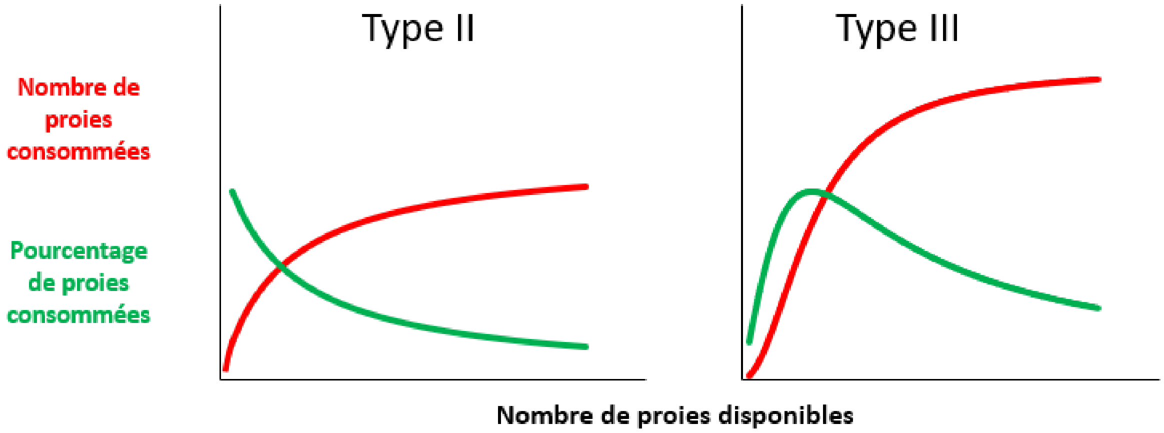

Figure 0.2 Différences entre les réponses fonctionnelles de type II et de type III pour le nombre de proies consommées (rouge) et le pourcentage de proies consommées (vert) en fonction du nombre de proies disponibles

Néanmoins, dans des forêts ripariennes composées principalement de frênes et d'érables argentés (*Acer saccharinum* Linnaeus), il a été prévu que l'action du castor pouvait entrainer, à long terme, une réduction de l'abondance des frênes accompagnée d'une augmentation de celle de l'érable argenté (Barnes & Dibble, 1988). Ceci est en contradiction avec une réponse fonctionnelle de type III. Il semble donc important de mieux caractériser la réponse fonctionnelle des castors, particulièrement face aux frênes, car celle-ci pourrait déterminer en partie la future composition des forêts ripariennes, notamment dans un contexte où le frêne commencera à devenir moins abondant. En effet, l'agrile du frêne est connu pour s'attaquer aux tiges de plus de 2 cm de diamètre (Aubin *et al.*, 2015), ce qui soulève une question importante. Est-ce que des peuplements résiduels pourraient survivre à l'invasion de l'agrile et recoloniser le milieu, ou bien est-ce que leur consommation par le castor aura au contraire un effet complémentaire à celui de l'agrile, et accélérera la disparition du frêne ?

1.3.2 Densités de castors

En plus du régime alimentaire et de la réponse fonctionnelle, il est également important d'évaluer si l'abondance ou la densité des frênes ont un impact sur la densité des castors, c'est-à-dire si ceux-ci présentent une réponse numérique (Gawlik, 2002). Pour comprendre comment et par quels mécanismes les densités des castors pourraient être affectées, il est indispensable de s'attarder davantage sur ce modèle biologique.

1.3.2.1 Structure sociale

Les castors sont des animaux sociaux vivant en groupes organisés autour d'une unité familiale composée d'un couple reproducteur, des juvéniles de l'année, et ceux de l'année précédente (Payne, 1982). Les jeunes quittent généralement l'unité familiale à l'âge de deux ans afin de s'implanter sur un territoire et de fonder leur propre colonie (Müller-Schwarze, 2011). Cependant, dans certains cas, notamment quand les densités de castors sont élevées, il n'est pas rare que les castors retardent leur dispersion d'une année supplémentaire, ce qui pourrait les rendre plus compétitifs lors de leur implantation (Mayer *et al.*, 2017b). Il a même été observé que chez le castor d'Europe, espèce très semblable au castor d'Amérique, les individus subalternes peuvent rester jusqu'à sept ans dans la colonie parentale. Plus la dispersion était retardée, plus les individus avaient de chance de sécuriser un territoire pour une longue période (Mayer *et al.*, 2017a). Si le castor est généralement admis comme étant une espèce socialement monogame, elle ne l'est pas nécessairement du point de vue génétique, puisque les copulations extra-paires ne sont pas rares pour cette espèce (Crawford *et al.*, 2008). Certaines études démontrent aussi que la composition des groupes pourrait être plus complexe dans certains cas, par exemple avec la présence de plusieurs femelles reproductrices, mais ces études semblent relativement anecdotiques dans la littérature (Bergerud & Miller, 1977; Busher *et al.*, 1983; Crawford *et al.*, 2008) et représentent probablement une réalité marginale.

1.3.2.2 Territorialité

Le castor est également une espèce territoriale. La notion de territoire a été définie pour la première fois par Noble (1939) comme étant « toute aire défendue », mais plusieurs dizaines de définitions existent (Maher & Lott, 1995). Ainsi, le territoire de certaines espèces est constitué de l'intégralité de leur domaine vital, comme c'est le cas chez le castor (Graf *et al.*, 2016). Des comportements territoriaux sont déployés pour la défense de cette aire (Hinde, 1956). Ces comportements varient selon les espèces et incluent des agressions physiques (Marler & Moore, 1988; Viera *et al.*, 2011), des marquages olfactifs (Rosell & Nolet, 1997), des vocalisations (Siracusa *et al.*, 2017) ainsi que des parades ou de signaux visuels (Burst & Pelton, 1983; Stehle *et al.*, 2017). Chez les castors, les individus des deux sexes marquent les limites de leur territoire en créant des buttes de marquage (Rosell & Nolet, 1997). Les buttes de marquage sont des amoncellements de boue que les castors font sur les rives de leur territoire, aux limites de celui-ci, et sur lesquelles ils vont déposer des sécrétions annales et du castoréum, une sécrétion odorante issue de glandes spéciales (Müller-Schwarze & Heckman, 1980a). Il a été démontré que les sites étaient moins susceptibles d'être colonisés par de nouveaux occupants s'ils étaient déjà délimités par des buttes de marquage (Müller-Schwarze & Heckman, 1980b). Bien que ce comportement territorial décourage certains intrus, les agressions conspécifiques sont fréquentes, surtout au printemps, lorsque de nouveaux individus tentent de s'installer (Mayer, Aparicio Estalella, *et al.*, 2020; Mayer, Frank, *et al.*, 2020). Les morsures que les castors s'infligent entre eux peuvent parfois même entraîner la mort de certains individus (DeStefano *et al.*, 2006). Les coûts et les investissements liés à la territorialité pèsent principalement sur les couples reproducteurs, ainsi que sur les individus cherchant à s'implanter sur un territoire, les individus subalternes (c'est-à-dire la progéniture du couple reproducteur) jouant un rôle minime dans la défense du territoire (Hohwieler *et al.*, 2018).

1.3.2.3 Modes possibles de régulation de la densité

Le fait que le castor soit une espèce sociale territoriale est très important pour comprendre comment sa densité est susceptible d'être modulée par la variation des ressources alimentaires. En effet, la densité d'une espèce sociale territoriale est égale à la taille moyenne du groupe (nombre moyen d'individus composant le groupe) divisée par la taille moyenne du territoire (superficie moyenne défendue par les groupes). La variation de la densité de la population peut donc venir d'une modification de l'un ou l'autre de ces facteurs, ou des deux.

Les castors étant territoriaux, une possibilité serait que la taille de leur territoire se régule en fonction de la qualité de l'habitat, qui est souvent en partie déterminée par la densité de ressources sur celui-ci (Johnson, 2007). Cette possibilité serait très probable, dans la mesure où la territorialité est généralement considérée comme le compromis entre les coûts et les bénéfices liés à la sécurisation d'un territoire. La possession d'un territoire peut être avantageuse pour un individu, lui permettant de mieux accaparer et sécuriser un ensemble de ressources, comme la nourriture ou les sites de reproduction (Maher & Lott, 1995). Toutefois, l'acquisition d'un territoire engendre également des coûts liés au temps et à l'énergie alloués à sa défense, qui ne pourront donc pas l'être pour d'autres activités (*e.g.* quête de nourriture), et représente une dépense énergétique. Une ressource ne devrait être défendue que si les bénéfices liés à cette ressource sont supérieurs au coût de sa défense (Peres, 1989). Il existe donc un compromis constant entre les coûts et bénéfices liés à la possession d'un territoire (Gill & Wolf, 1975; Wyman & Hotaling, 1988). Ce compromis est généralement exprimé à travers la taille du territoire. Plus le territoire sera grand, et plus la quantité de ressources présente dans celui-ci sera importante. Cependant, un grand territoire est beaucoup plus coûteux à défendre, parce qu'il sera potentiellement soumis à un plus grand nombre d'intrusions, et nécessitera donc un plus grand nombre de comportements agressifs pour le défendre (Schoener, 1983). Passé un certain seuil, le bénéfice tiré de l'agrandissement du territoire deviendra inférieur au coût de son maintien. Ce compromis constant implique donc une taille de territoire optimale (Hixon, 1980; Praw & Grant, 1999; Schoener, 1983). La taille optimale d'un territoire sera dépendante de sa qualité, ce qui explique donc que l'augmentation de la qualité de l'habitat puisse engendrer un rétrécissement des territoires ; ou que la diminution de la qualité de l'habitat puisse amener à l'agrandissement des territoires (Calsbeek & Sinervo, 2002). Les territoires peuvent ainsi être vus comme des disques élastiques pouvant être compressés, mais leur compression requiert une pression de plus en plus forte au fur et à mesure qu'ils rétrécissent (Huxley, 1934). De nombreuses études empiriques ont montré que la taille des territoires n'est pas fixe, et qu'ils peuvent rétrécir, soit par l'augmentation de la densité d'une population (Lindeman *et al.*, 2015), ou par l'augmentation de la qualité d'un habitat (Calsbeek & Sinervo, 2002). Lorsque la densité ou la qualité de l'habitat augmente, la taille des territoires diminue jusqu'à atteindre une taille de territoire minimale, c'est-à-dire la taille de territoire limite pour laquelle le bénéfice est encore supérieur aux coûts (Grant *et al.*, 2017; Wood *et al.*, 2012). Le castor étant une espèce très territoriale, il semble cohérent de penser que la modification de la qualité de l'habitat (potentiellement la réduction de celle-ci via la disparition des frênes) pourrait entrainer une augmentation de la taille moyenne des territoires, afin que les castors maintiennent une quantité minimale de ressources nécessaire à leur survie et à leur reproduction. Il a déjà été démontré, par exemple pour les loups, que la qualité de l'habitat va déterminer la taille des territoires, mais pas la taille des groupes (Kittle *et al.*, 2015).

Cependant, la régulation de la densité pourrait théoriquement passer par la taille des groupes, et non pas par la taille des territoires. Certaines hypothèses écologiques évoquent en effet qu'un tel processus serait envisageable, comme l'hypothèse de la dispersion des ressources qui a été largement utilisée pour décrire la vie en groupe des carnivores sociaux (Macdonald, 1983) et a souvent été utilisée pour comprendre les causes de la vie en groupe (Johnson *et al.*, 2002). Depuis sa création, cette hypothèse a également été utilisée pour comprendre la socialité d'autres espèces, y compris les capybaras, d'autres rongeurs sociaux (Herrera *et al.*, 2011). L'une des prévision centrales de cette hypothèse est que la taille du territoire et la taille du groupe sont indépendantes (Johnson *et al.*, 2002; Robertson *et al.*, 2015). La taille du territoire sera en effet déterminée par la dispersion des ressources, tandis que la taille du groupe sera déterminée par la qualité de ces ressources. Cette hypothèse a déjà été démontrée pour certaines espèces, comme le blaireau d'Europe, qui répondait à ces prévisions (Kruuk & Parish, 1982). Cependant, les exemples d'espèces répondant parfaitement à ces prévisions sont rares.

Enfin, il serait possible que la densité soit régulée par une modification à la fois de la taille des groupes et de la taille des territoires. Il a par exemple été montré que, pour les espèces répondant à une distribution despotique idéale, l'augmentation de la qualité de l'habitat pouvait à la fois engendrer une diminution de la taille du territoire et une augmentation de la valeur adaptative (Calsbeek & Sinervo, 2002). Pour une espèce sociale territoriale comme le castor, pour laquelle le groupe est composé d'un couple reproducteur et de leur descendance, il est probable que la taille du groupe puisse représenter une bonne indication de la valeur adaptative. En effet, la taille du groupe sera en partie déterminée par le succès reproducteur du couple, et par la survie des juvéniles lors des premières années de vie. Par ailleurs, comme cela a été prouvé, les individus subalternes qui resteraient plus longtemps que les deux années minimales seraient plus probables de s'implanter sur un territoire durablement (Mayer *et al.*, 2017a) et donc de se reproduire à leur tour ;

leur présence dans un groupe serait donc également une indication d'une valeur adaptative élevée pour le couple reproducteur.

Pour le castor, il n'est pas encore certain du mécanisme par lequel les densités seront modifiées. En effet, aucune étude n'a encore testé ces hypothèses alternatives concernant les trois mécanismes possibles. Les études existantes ont pour le moment porté directement ou indirectement sur la taille des groupes ou la taille des territoires, mais pas sur les deux. Ainsi, il a déjà été montré par Campbell *et al.* (2005), que la taille des territoires ne semblait pas être négativement corrélée à la qualité de l'habitat pour les castors, mais aucun test n'avait été réalisé sur la taille des groupes dans cette étude. Smith (1997) a établi que le nombre de juvéniles observé était plus grand lorsque les espèces favorites du castor étaient abondantes, ce qui impliquerait un effet potentiel sur la taille des groupes, mais n'a pas testé si cela avait également un effet sur la taille des territoires. Fryxell (2001) a également pu démontrer que la taille des groupes était effectivement directement liée à la qualité de l'habitat. Cependant, deux études ont eu des résultats différents. En effet, il a également été montré que la densité de colonies était dépendante de la qualité de l'habitat (Bergman *et al.*, 2018; Smith & Tyers, 2012). Une densité de colonies qui augmente implique donc probablement une taille de territoire qui peut décroitre avec l'augmentation de la qualité de l'habitat. Dans la mesure où les mécanismes régissant les densités de castors sont encore inconnus, mais qu'il semble que la disparition des frênes pourrait avoir des conséquences sur la qualité de l'habitat, et donc sur les densités de castors.

Il apparait important de déterminer comment les densités de castors pourraient être modifiées par l'invasion de l'agrile du frêne. Cette information est capitale, puisque les castors sont connus comme pouvant couper la majorité des arbres qu'ils préfèrent dans certaines conditions, impactant donc grandement la composition forestière locale (Johnston & Naiman, 1990). Une modification de la densité par la taille du groupe pourrait donc avoir des effets différents d'une modification par la taille du territoire localement. Cette dichotomie est représentée d'une manière simplifiée ci-dessous (figure 0.2) avec quatre groupes de castors de taille équivalente avant la disparition des frênes (figure 0.2a), pour lesquels la qualité de l'habitat diminue lors de l'invasion par l'agrile du frêne. La diminution de la qualité de l'habitat pourrait entraîner des répercussions sur la taille du groupe (figure 0.2b) ou sur la taille du territoire (figure 0.2c). Si la qualité de l'habitat influence la taille du groupe, le nombre moyen de castors par groupe pourrait diminuer avec la disparition des frênes, dépendamment des essences de remplacement. Comme les castors sont des animaux très territoriaux (Herr & Rosell, 2004; Nolet & Rosell, 1994; Rosell & Thomsen, 2006), les groupes de castors ne devraient pas partager leurs zones d'alimentations avec d'autres groupes, cela signifie que les peuplements (notamment les plus attractifs après la disparition des frênes) devraient être ciblés par des groupes de castors peu nombreux (Figure 0.2b) en comparaison à l'autre option. Alternativement, si la qualité de l'habitat a un effet sur la taille des territoires, les groupes pourraient conserver le même nombre d'individus en agrandissant leur territoire. Dans ces conditions, les peuplements les plus attractifs auront davantage de chances d'être entièrement consommés, car fréquentés par des groupes plus nombreux (Figure 0.2c). Bien entendu, ces deux options (peu de grands groupes ou beaucoup de petits groupes) ne présenteraient pas de différence pour la quantité totale de bois consommée par les castors à large échelle. Cependant, à fine échelle, cette distinction permettrait de mieux comprendre le risque qu'encourront les peuplements qui seront privilégiés par les castors pour s'alimenter après la disparition du frêne. Finalement, une modification de la densité des castors à la fois par la modulation de la taille du groupe et celle du territoire aurait probablement un effet intermédiaire entre ceux schématisés aux figures 0.2b et 0.2c.

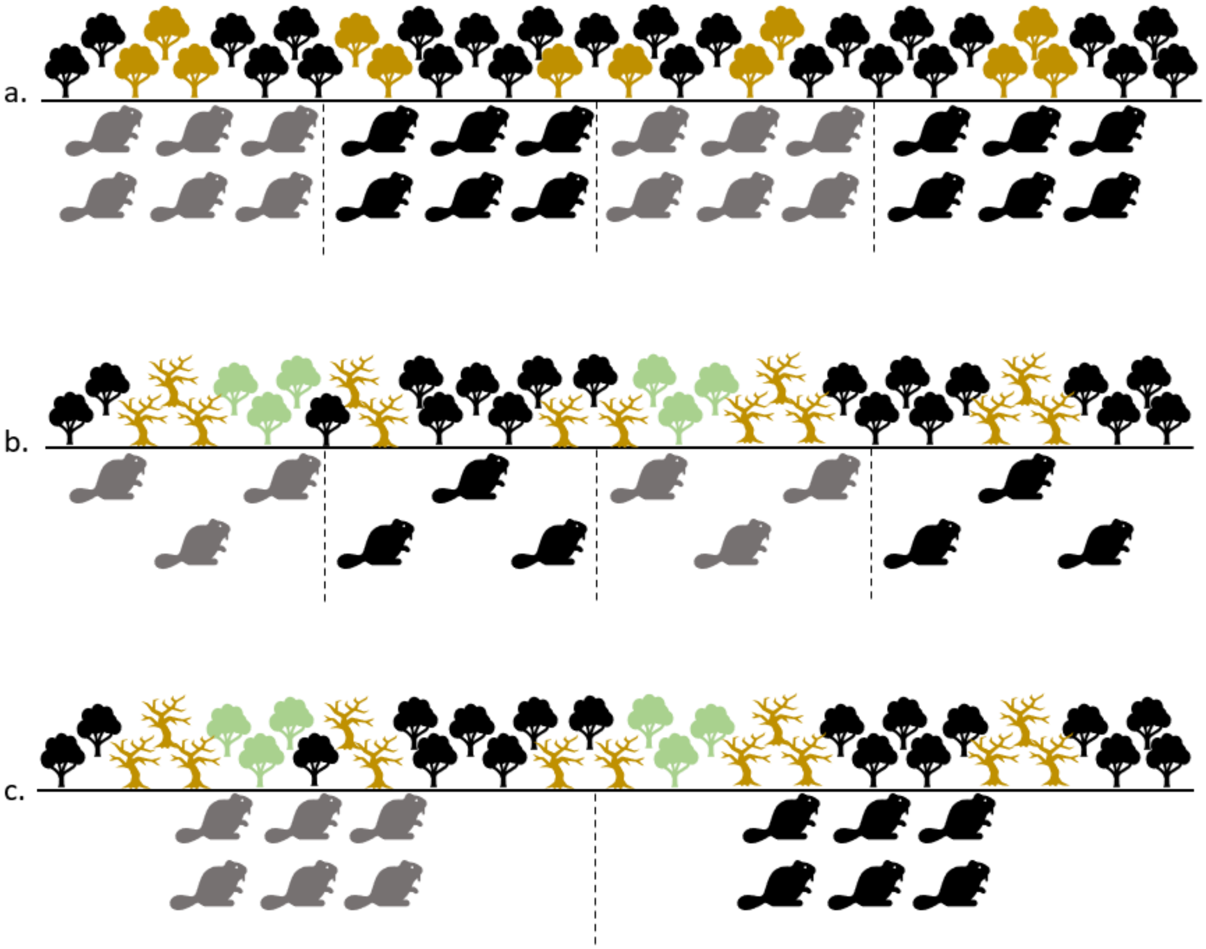

Figure 0.3 Schéma représentant quatre colonies de castors dans un habitat dominé par le frêne (arbres marrons) avant l’invasion de l’agrile (panneau a.), puis simulant l'effet de la diminution de la qualité de l'habitat entrainée par la disparition du frêne sur la taille des groupes (panneau b.) ou sur la taille des territoires (panneau c.). Les arbres verts représentent des peuplements qui deviennent les plus attractifs pour les castors après la disparition du frêne, et qui ne seraient pas influencés de la même façon selon le scénario choisi.

1.4 Site d’étude

L’ensemble des inventaires et expérimentations réalisées dans le cadre de ce doctorat se sont déroulées au parc national de Plaisance. Ce parc de 28 km^2 représente un site d’étude très favorable aux questions que nous tenterons d’aborder, et ce pour plusieurs raisons.

Le parc national de Plaisance est composé d'une multitude de péninsules, de baies, et d'iles, faisant en sorte qu'une grande partie des 400 ha de forêt peut être considérée comme forêt riparienne, en raison des inondations annuelles. La composition du parc est également très favorable à la question de recherche posée ici, puisque les frênes y sont dominants. Environ un quart de la surface terrière de la forêt est composée des trois espèces de frênes (*F. pennsylvanica*, Marshall ; *F. americana*, Linnaeus ; et *F. nigra*, Marshall), et un autre quart d'érables (*A. saccharinum* Linnaeus ; *A. rubrum* Linnaeus ; et *A. freemanii*, Murray). Le reste de la forêt est très diverse, et représente une quarantaine d'espèces d'arbres indigènes du Québec. Même si la forêt est dominée par les frênes, elle reste très hétérogène, et il n'est donc pas difficile d'y trouver des peuplements dans lesquels les frênes représentent quasiment toute la surface terrière, et d'autres dans lesquels ce genre est absent. Cette hétérogénéité permet donc l'échantillonnage de tout le gradient d'abondance des frênes qui peut être présent dans les forêts de ce biome, ce qui est déterminant pour la présente étude. Enfin, le parc possède l'une des plus hautes densités de castors en terres publiques du Québec, lorsque comparé avec les inventaires officiels (Lafond *et al.*, 2003). Les inventaires des castors dans le parc montrent clairement une augmentation exponentielle au fil du temps : de 40 huttes en 2007, à 80 en 2014 et à près de 120 en 2018. L'ensemble de ces facteurs fait donc du parc national de Plaisance un laboratoire naturel idéal pour déterminer l'effet qu'aura la disparition des frênes sur la biodiversité des forêts ripariennes.

1.5 Objectif du doctorat

D'un point de vue général, ce doctorat a pour but de déterminer le rôle des frênes sur la biodiversité des forêts ripariennes. Du fait de son rôle déterminant pour la composition forestière, le castor sera ici étudié, afin de savoir comment son régime alimentaire et ses densités de population pourraient être modifiés par la disparition des frênes. Par ailleurs, les invertébrés étant à la fois très diversifiés, constituant l'une des bases du réseau trophique, et ayant des rôles écologiques majeurs, ils seront choisis pour essayer d'établir quels effets la disparition des frênes pourraient avoir sur la biodiversité animale.

Le premier chapitre de ce doctorat détermine la place exacte des frênes dans le régime alimentaire du castor dans les forêts ripariennes dominées par cette essence. Nous documenterons notamment quelles essences sont sélectionnées et quelles essences sont évitées dans ce type de forêts. Nous déterminerons également l’ordre des préférences, en comparant la probabilité de consommation de chaque essence à celle du frêne, ce qui pourrait permettre de cibler quelles essences sont les plus susceptibles de remplacer les frênes dans l’alimentation du castor. Enfin, nous testerons si les probabilités de consommation des genres les plus répandus dans le site d’étude dépendent de la densité de frêne, afin de prévoir comment les probabilités de consommation de chaque essence vont être modifiées lors de la disparition des frênes.

Pour le deuxième chapitre, nous déterminerons si les frênes ont le potentiel d’influencer les densités de castors, et par quels mécanismes. Les densités de frênes seront utilisées pour expliquer à la fois la taille des territoires et la taille des groupes de castors, afin de déterminer si cette densité influence la taille du groupe, du territoire, ou les deux. Cela permettra de mieux comprendre comment les populations de castors risquent de répondre à la disparition des frênes, car la densité de ces rongeurs affectera nécessairement les forêts ripariennes.

Le troisième chapitre de ce doctorat visera à mesurer si c’est bien les espèces de frênes qui déterminent le plus le caractère labile de la litière dans une forêt composée majoritairement de frênes et d’érables. Nous déterminerons si la disparition du frêne a le potentiel d’avoir un effet sur les communautés d’invertébrés, que ce soit sur la diversité des taxons présents, sur l’assemblage des communautés, ou même sur leur diversité taxinomique.

Pour finir, nous tenterons de mettre en relation les différents résultats obtenus dans ces trois chapitres pour déterminer l’importance des frênes pour la biodiversité des forêts ripariennes, et l’avenir de celles-ci après la disparition engendrée par l’agrile du frêne.

CHAPITRE 1

STUCK BETWEEN THE MANDIBLES OF AN INSECT AND OF A RODENT: WHERE DOES THE FATE OF ASH-DOMINATED RIPARIAN TEMPERATE FORESTS LIE?

Publié dans *Forests* : Rosner, S., Dupuch, A., & Lorenzetti, F. (2022). Stuck between the mandibles of an insect and of a rodent: where does the fate of ash-dominated riparian temperate forests lie? *Forests*, *13*(11), 1760. https://doi.org/10.3390/f13111760

Suite aux commentaires du jury de thèse, certaines améliorations ont été apportées au chapitre, qui ne correspond donc pas entièrement à l'article publié.

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RÉSUMÉ

Le castor (*Castor canadensis* Khul) est une espèce clé connue pour façonner la composition des forêts ripariennes. Les frênes (*Fraxinus* spp.) peuvent être abondants dans ces forêts. Cependant, l'invasion de l'agrile du frêne (*Agrilus planipennis* Fairmaire) en Amérique du Nord menace leur survie. La disparition des frênes aura un impact important sur la composition de la forêt en zone riparienne en soi. On ne sait pas encore quelles seront les conséquences pour la forêt résiduelle si de plus le frêne joue un rôle important dans le régime alimentaire du castor. Des parcelles d'inventaires sur un gradient de densités de frênes ont été échantillonnées dans le parc national de Plaisance, Québec, Canada, afin de mesurer si (1) les arbres et les gaules de ce genre étaient sélectionnés ou évités par les castors, (2) si d'autres genres avaient une probabilité plus faible ou plus grande d'être consommés par rapport au frêne, et (3) si la densité de frênes pouvait affecter la probabilité de consommation d'autres genres. De tous les genres présents dans le parc, les frênes ont été sélectionnés par les castors dans le plus grand nombre de parcelles. Seuls deux genres, *Carpinus* et *Populus*, avaient une probabilité plus élevée d'être consommés que le frêne. Ces genres ne sont pas abondants dans le parc, de même que dans les forêts ripariennes du biome tempéré, et ne sont donc pas de bons candidats pour remplacer le frêne comme aliment de base des castors. Le genre le plus abondant dans les forêts riveraines tempérées, avec le frêne, est l’érable (*Acer* spp.). Dans cette étude, les arbres du genre *Acer* n'ont pas été sélectionnés et, comme pour les gaules d’érables, ils sont moins susceptibles d'être consommés que les frênes. Des résultats mitigés ont été obtenus concernant les genres qui pourraient devenir plus susceptibles d'être consommés lorsque la densité des frênes diminuera. Il semblerait que la disparition du frêne n'entraînerait pas un passage à un seul ou à quelques genres dans le futur, ce qui pourrait être dû à la grande diversité des genres présents dans les forêts riveraines tempérées. Cependant, le frêne pourrait ne pas disparaître complètement en raison de sa capacité à faire des rejets de souche après la mort de la partie aérienne des arbres. Ce scénario est discuté à la lumière de la susceptibilité des tiges de frêne de taille intermédiaire à être colonisées par l'agrile du frêne et de la plus grande probabilité que les castors se nourrissent de ces tiges de même taille.

Mots-clés: *Castor canadensis*; *Fraxinus* spp.; Agrile du frêne; Comportement alimentaire; Forêts ripariennes; Biome tempéré

ABSTRACT

The beaver (*Castor canadensis* Khul) is a key species that is known to shape the composition of riparian forests. Ash trees (*Fraxinus* spp.) can be abundant in these forests. However, invasion by the emerald ash borer (*Agrilus planipennis* Fairmaire) in North America threatens their survival. The disappearance of ash will have a large impact on the riparian forest tree species composition. It is not known what the consequences would be for the remaining forest if ash plays an important role in the beaver diet. Inventory plots across a ash gradient were measured in Plaisance National Park, Quebec, Canada, to collect data and to establish if (1) trees and saplings of this genus were selected or avoided by beavers, (2) if other genera had a lower or a greater probability of being consumed compared to ash, and (3) if ash density could affect the probability of consumption of other genera. Of all genera present in the park, ash trees were selected in the highest number of plots. Only two genera, *Carpinus* and *Populus,* had a higher probability of being consumed than ash. These genera are not abundant neither in the park nor in riparian forests of the temperate biome, and thus are not good candidates to replace ash as a staple for beavers. The most abundant genus in riparian temperate forests, along with ash, is *Acer*. In this study, *Acer* trees were not selected, whereas *Acer* saplings were less likely to be consumed than ash. Mixed results were obtained about genera that could become more likely to be consumed as ash densities decrease. Given the high diversity of genera present in temperate riparian forests, it seems likely that the disappearance of ash will not cause a switch to a single or a few genera in the future. However, ash may not disappear completely due to its capacity to sprout following the death of the aboveground portion of ash trees. This scenario is discussed in light of the susceptibility of intermediate-sized ash stems to be colonized by the emerald ash borer and of the greater likelihood of beavers to feed on these same-sized stems.

Keywords: *Castor canadensis*; *Fraxinus* spp.; Emerald Ash Borer; Feeding behavior; Riparian forests; Temperate biome

1.1 Introduction

The emerald ash borer (*Agrilus planipennis* Fairmaire) (EAB) is an invasive species to North America (Haack *et al.*, 2002) and Europe (Musolin *et al.*, 2021). All North American ash species (*Fraxinus spp.*) are susceptible to be attacked by the EAB, but green ash (*F. pennsylvanica* Marshall), white ash (*F. americana* Linnaeus), and black ash (*F. nigra* Marshall) are the preferred hosts on which EAB is able to complete its life cycle (MacFarlane & Meyer, 2005; Poland *et al.*, 2015). The consequence of this attack is that trees of those species die after a few years (Knight *et al.*, 2013). These three species are the most abundant ash species and can make up to a high proportion of the canopy of the eastern temperate forests in both the USA (*Www.Fs.Fed.Us*, 2022) and Canada (*Www.Canada.Ca*, 2022). This highlight the dramatic effects that EAB can have on many North American forest ecosystems.

Eastern North America, riparian forests are often dominated by ash spp. and will be highly impacted by EAB (Engelken & McCullough, 2020). Riparian forests are recognized to playmajor ecological roles as they are the interface between terrestrial and aquatic ecosystems, making them critical transition zones (Ewel *et al.*, 2001). Indeed, ecosystems services provided by riparian forests range from flood regulation to sediment retention to the flux of nutrients (Gregory *et al.*, 1991; Naiman & Decamps, 1997). Furthermore, riparian forests are known to harbour a high biodiversity of animal and plant species (Forio *et al.*, 2020; Maisonneuve & Rioux, 2001; Paine & Ribic, 2002). Despite their small size, their roles expand beyond their limits, making these areas important targets for conservation efforts (Hunter *et al.*, 2017).

The high animal biodiversity in riparian forests , can be partially attributed to ash trees. Gandhi & Herms, (2010b) reported that 43 arthropod species native to North America are completely dependent on ash spp., either to feed or to reproduce. Furthermore, they found in their literature review that 30 more species would become moderately to highly at risk, and that more than 200 other species could potentially be impacted as well by the extinction of ash trees in North America. A recent study also highlighted the potential effect of the disappearance of ash spp. on mammal and bird communities due to the risk of conversion of forested to non-forested wetlands and a concomitant decrease in connectivity for forest species (Grinde *et al.*, 2022).

A key species that have a profound effect on riparian forests and its diversity is the beaver (Nummi *et al.*, 2019; Stoffyn-Egli & Willison, 2011). Beavers are often coined as ecosystem engineers, mainly because of the dams they built and the new water bodies they generate, which provides habitats for plant and animal species. However, their role in shaping the environment in which they live extend to the riparian forests next to the newly generated water bodies. There are two species of beavers, one native to Europe (the European beaver, *Castor fiber* Linnaeus), and the other to North America (the American beaver, *Castor canadensis* Khul). Both species are very similar, with respect to their morphology or general behavior (Rosell *et al.*, 2005; Zavyalov, 2014). Therefore, the literature on both species is relevant to questions addressing resource selection and feeding behavior. Both species have been shown to be choosy generalists (Busher, 1996; Vorel *et al.*, 2015) which means that despite being able to feed on a very wide range of plant species, they exhibit a high preference for some items over others. Although preference may depend on the local abundance of certain species, two tree genera are recognized as prefered food items for beavers: poplars (*Populus* spp.) and willows (*Salix* spp.) (Hall, 1960; Smith & Tyers, 2012; Vorel *et al.*, 2015).

Beavers generate gaps in the riparian forest (Johnston & Naiman, 1990) that can be filled with plant species adapted to these disturbance dynamics, such as some ash or maple (*Acer* spp.) (Cook, 2005; King & Antrobus, 2005). However, by selecting some items over others, beavers favor the growth, and indirectly the relative abundance, of less selected items, thus affecting the future composition of the forest canopy (Johnston & Naiman, 1990). In North America, this replacement process has often been reported, especially in mixed woods of the boreal forest where poplar species are highly selected, accelerating forest composition towards coniferous dominance, or towards a shrub cover of *Alnus* or *Corylus* when coniferous species are rarely present (Donkor & Fryxell, 2000; Johnston & Naiman, 1990; Martell *et al.*, 2006; Naiman *et al.*, 1986, 1988). However, in temperate deciduous forests, especially when poplars and willows are absent or at low densities, selection by the beaver is not clear. Depending on the studies, *Prunus* spp., *Fagus* spp., *Acer* spp., *Betula* spp., *Quercus* spp., *Carpinus* spp., *Alnus* spp. or *Ostrya* spp. are reported as selected, but not systematically (Busher, 1996; Müller-Schwarze *et al.*, 1994; Raffel *et al.*, 2009; Rossell *et al.*, 2014). Ash is also among the genera that can be positively selected by beavers (Müller-Schwarze *et al.*, 1994) but this is not always the case (Johnston & Naiman, 1990; Raffel *et al.*, 2009). The selection of ash spp. appears to depend on whether or not the beaver's favorite food items are present. These discrepancies in the literature highlight the need to better understand the importance of ash spp. in beavers' diet, given how species of this genus are instrumental in supporting biodiversity in riparian temperate forests.

The fact that ash spp. can be highly selected by beavers in some areas, to a point where a drastic decrease in density is predicted (Barnes & Dibble, 1988), raises the question of what the disappearance of mature ash trees in the riparian forests caused by the EAB may have on the foraging tree selection by beavers, especially if their favorite items becomes scarce. Indeed, if ash trees are one of the main food source for beavers, a sudden decrease in their density could potentially modify their feeding behavior with unknown consequences for other tree and shrub species in riparian forests. Because the results of the beaver feeding behavior, in combination with the current invasion of EAB, are not well anticipated, it seems important to have a better understanding of the importance of ash spp. in the diet of the beaver. Indeed, understanding its importance would allow to be better prepared for the potential disappearance of ash spp. and its consequences. Furthermore, this could help to predict how the pressure on the riparian temperate forests exerted by the feeding behavior of beavers may be modified in the near future.

This study had three main objectives: (1) to establish whether ash spp. - but also other genera present in the diverse riparian forests at the study site - were selected for or selected against by the beavers; (2) to determine the odds for a genus to be consumed by the beavers compared to ash spp. and (3) to examine, as ash spp. abundance decreases from high to low, whether some genera could exhibit a change in their probability of being consumed.

1.2 Materials and Methods

1.2.1 Study site

This study was conducted in Plaisance National Park, Quebec, Canada. Created in 2002, it is a relatively small conservation park in Quebec, with an area of 28 km^2. Located along the Ottawa River (Figure 1.1), which has one of the highest river discharges in Quebec, the park is made up of a multitude of small islands and peninsulas with a cumulative length of banks of more than 100 km. Inland waters consist of several ponds and swamps. Only 400 ha of the emerged land in the park are classified as forest from aerial inventories by the Quebec Ministry of Forests, Wildlife and Parks. An extensive land inventory of the park's forests conducted prior to this study showed that there are more than 40 tree species, representing around two-thirds of the native tree species found in Quebec (F. Lorenzetti, *unpublished results*). Although the forested area of the park is small but diverse, it was estimated that half of the basal area of the trees (⩾ 10 cm of DBH) is equally composed of maple spp. (*Acer saccharinum* L., *A. rubrum* L. and *A.* × *freemanii* E. Murray) and of ash spp. (*F. pennsylvanica*, *F. americana*, and *F. nigra*). However, the densities of maple and ash vary from scattered trees to dominant in the various stands.

The density of beavers in the park is considered to be among the highest in Quebec in unexploited areas when compared to official inventories (Lafond *et al.*, 2003). The inventories of the beaver lodges in the park clearly show an exponential increase over time: from 40 lodges in 2007, to 80 in 2014, and to almost 120 in 2018. The first two inventories were realized by the park staff with an aerial inventory, and the third by S. Rosner by boat. All inventories involved reaching close to each lodge to mark its location. Two run-of-the-river dams on the Ottawa River, one upstream and one downstream of the park, regulate water levels. Although variations in water levels are dampened by dams, spring floods are recurrent, allowing the beavers to swim sometimes deeply into the flooded riparian forest. The study site in Plaisance National Park was considered to be one of the best possible opportunities to assess the importance of ash spp. in the diet of beavers in riparian forests of the temperate deciduous biome. Indeed, in addition of being representative of the compositional diversity of the forest of the ecological region of the Outaouais and St-Lawrence River (Major *et al.*, 2012), ash spp. in the forest of the park ranges from low relative abundance to dominance, making it an ideal site to address the importance of that genus in the diet of beavers. Furthermore, the absence of beaver dams in the park ensures that most of the gathered stems are used as food, except for the small portion used to build the lodges.

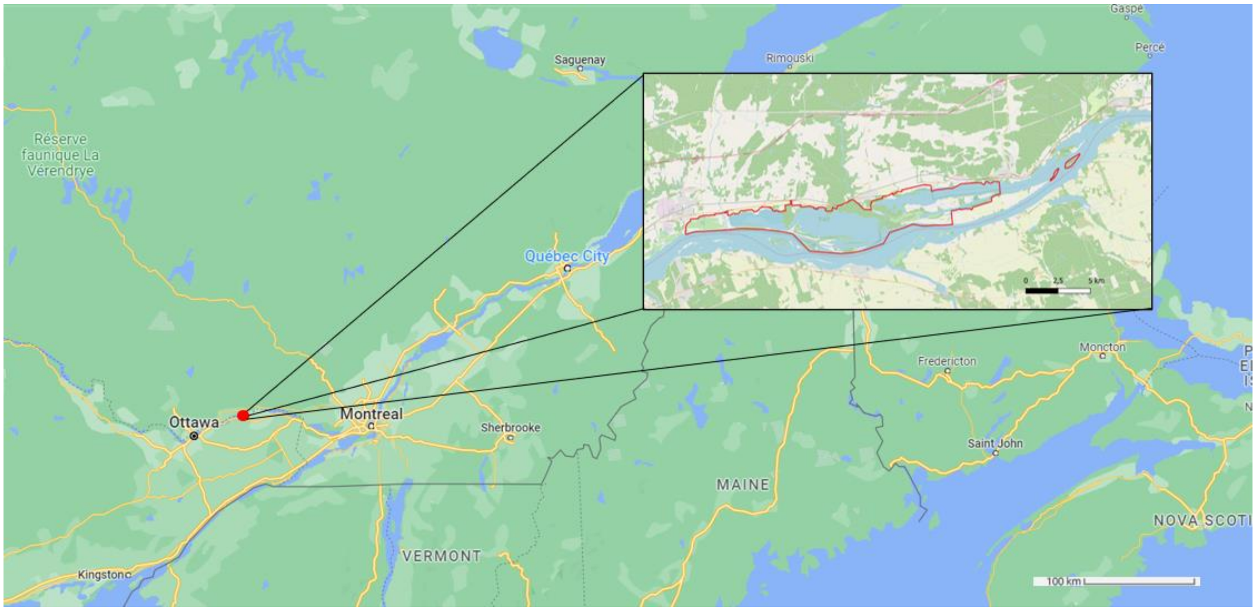

Figure 1.1 Location of Plaisance National Park on the Ottawa River, Quebec, Canada. Insert: park limits are drawn with a red line. Maps are based on images from Google, 2022 (large scale) and OpenStreetmap (small scale).

1.2.2 Study design

A total of 24 plots were set across the riparian forest of the park, and inventoried over a period of four weeks in the summer of 2019, with two main goals: (1) to be representative of the tree composition found in the park, and (2) to cover an ash spp. gradient based on the basal area among plots so to make it possible to investigate if the abundance of ash influences the beaver's selection of tree and shrub items. The plots were set to be at least 150m apart from each other. Each plot was 1500 m^2 in size: 30 meters along the shoreline and 50 meters deep into the forest (Figure 1.2). For every tree and shrub, the diameter was measured at 30 cm above ground since it appeared to be the typical height at which beavers cut most trees. Within each plot, every tree with a diameter > 9 cm at that height was identified to the species, its diameter was measured and its distance from the shoreline was assigned to one of the five 10-meter classes (0-10 m; 10.1-20 m; 20.1-30 m; 30.1-40 m; 40.1-50 m). Each tree was classified as consumed or not consumed. A tree was considered consumed if completely or almost completely, felled by beavers or if beavers had started to fell it and had removed most of the bark. Non-consumed trees were those with their bark intact or those that presented only a few bite marks.

Consumption of saplings and shrubs by beavers was also measured in subplots of the 24 main plots. Each main plot was subdivided into 60 subplots 5m in diameter, 10 rows of 6 subplots parallel to the shoreline (Figure 1.2). One subplot was randomly selected from each row. As for the trees, this allowed to estimate consumption (*i.e.*, consumed or not consumed) in relation to distance to the shoreline. All saplings and shrubs with a diameter at 30cm above ground greater than 1cm but less than 9cm were identified to the species, assigned to a distance class from the shoreline, and categorized as consumed (*ie*, a stem completely cut by a beaver) or not (*ie*, undamaged stem by beavers). Stump sprouts were counted as individual saplings. The diameter was assigned to one of the four following classes: [1-3cm]; [3.1-5cm]; [5.1-7cm]; [7.1-9cm]. Sapling and shrub stems from the 10 subplots were added and the sum per genus and per plot was used in the analyses. The subplot identity was only used as a proxy for the distance to the shore (for example, subplot 1 was always 0 to 5 meters from the shore, and subplot 10 was always 45 to 50m from the shore).

Due to the great heterogeneity of the forests in the park, and because the plots were selected to represent a large gradient of ash spp. sapling and tree densities, tree composition varied from one plot to another. Ash spp. was the only genus that was present as saplings and trees in each of the 24 plots. Ash spp. sapling abundance varied from 1 to 116 stems per plot (or 51 to 5908 stem/ha), with a median of 21 stems (or 1070 stem/ha). Ash tree abundance ranged from 16 to 258 stems per plot (or 107 to 1720 stems/ha) with a median of 63 stems (or 420 stems/ha). Tree genera that were present in the highest number of plots, after ash spp., were *Acer* (23 plots, range 3 to 64 stems, median = 21), *Ulmus* (21 plots, range 1 to 18 stems, median = 7), *Quercus* (16 plots, range 2 to 34 stems, median = 6), *Tilia* (14 plots, range 1 to 36 stems, median = 8), and *Populus* (13 plots, range 1 to 12 stems, median = 4). The eight other tree genera present in the inventories were found in less than 10 plots. Overall, from 3 to 11 genera were found per plot, with six genera being the median number. In the case of the shrubs and saplings, *Ilex* (21 plots, range 2 to 192 stems, median = 43) and *Cornus* (19 plots, range 1 to 101 stems, median = 11) were the most frequent genera after ash ssp. followed by *Prunus* (14 plots, range 1 to 54 stems, median = 8), *Acer* (13 plots, range 1 to 43 stems, median = 4), *Tilia* (11 plots, range 2 to 23 stems, median = 8) and *Ulmus* (10 plots, range 1 to 4 stems, median = 1). Over the 20 genera identified for this layer, 13 were found in less than 10 plots.

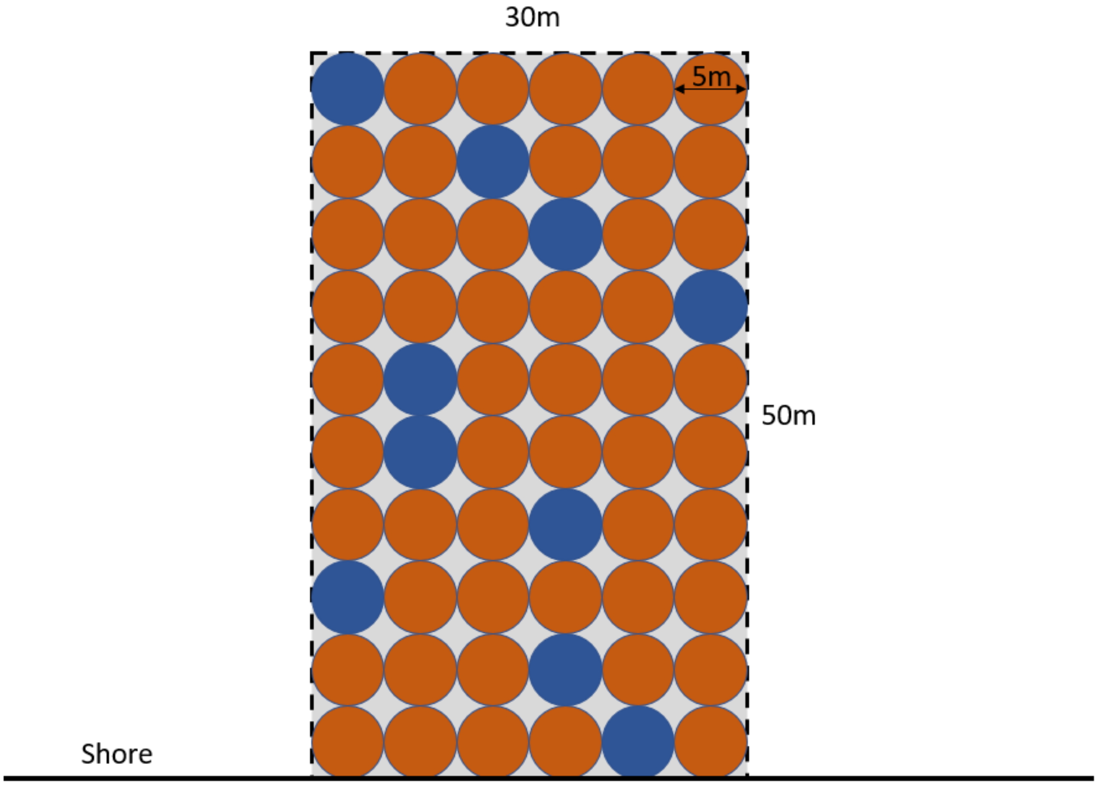

Figure 1.2 Schematic representation of a sampling plot (1500 m^2 in size) with randomized subplots for the assessment of beaver consumption of trees (whole-plot level) and of saplings and shrubs (subplot level). All trees with a diameter >9 cm at 30 cm above ground were sampled. Blue circles represent randomly selected subplots (5m in diameter) in which all saplings and shrubs <9cm in diameter at 30 cm above ground were sampled. One subplot in each of the 10 rows parallel to the shoreline was sampled.

1.2.3 Statistical Analysis

Although each tree, shrub and sapling was identified at the species level, all statistical analyses were performed at the genus level to increase sample size per genus. All analyses were performed separately for the trees and for the saplings and shrubs. The full data set was composed of 3423 tree stems counted over 14 genera (range 6 to 1992 stems per genera) and of 3840 shrub and sapling stems counted over 20 genera (range 1 to 1371 stems per genera). Depending on the objective, statistical analyses were performed at the genus level (objective 1) or at the stem level (objectives 2 and 3).

To establish which genera were selected for or against by the beavers (objective 1), a Jacobs index value (Jacobs, 1974) was calculated for each plot for the most abundant genera. In fact, eight tree genera represented 98% of the tree stems and nine shrub and sapling genera accounted for 95% of stems in that stratum. A significant positive value of the Jacobs index indicates that the item is positively selected by the beavers, meaning that it is consumed proportionally more than it is available among all the stems presents. On the opposite, an item is selected against if the Jacobs index is significantly negative, meaning that the item is consumed proportionally less than it is available among all the stems presents. Significance was examined on a permutation-based Chi-square test.

To assess the odds of non-ash spp. being consumed relative to ash spp. (Objective 2), mixed effects logistic regressions were performed in which were included only the genera that had been consumed in at least five of the 24 plots *i.e.*, nine genera out of 20 for the saplings and shrubs and five genera out of 14 for the trees. These genera represented a large proportion of available stems (95% of the saplings and shrubs, and 90% of the trees) as well as of the consumed stems (93% of the saplings and shrubs, and 96% of the trees). To estimate the probability of a tree (n = 3068), a sapling or shrub (n = 3636) of non-ash genera to be consumed (coded ‘1’) or not (coded “0”) relative to ash spp., the genus of each stem was included as a fixed effect variable in the models. This variable was coded as a dummy variable with ash genus set as the reference class in the analyses. The distance to the shore, as well as the diameter of the stem, are known to influence the feeding behavior of beaver (Deardorff & Gorchov, 2021). Therefore, these two variables were included as fixed effects in the models to estimate the odds of each genus would be consumed relative to ash spp. while factoring in the effects of these two variables. The distance to the shore was set as a numeric variable (1 to 5 for the 10m classes of the tree models, and 1 to 10 for the 5m classes of the sapling and shrubs models). To test for a possible quadratic effect of the diameter on the probability of stems being consumed (see Raffel *et al.*, 2009), the variable diameter squared was also added as a fixed variable in the models. For saplings and shrubs, the diameter was included as a numeric variable based on the mid-class value. Given that no quadratic response has been detected for the trees, this variable was dropped from further tree models, but was kept for the shrubs and saplings as it was significant for that stratum. The effect of the interaction between distance and diameter was tested, as well as the interaction between genus and diameter, or genus and distance, on the probability of a stem being consumed, and none turned out to be significant. The distance to the nearest lodge might be a factor influencing the feeding habits of beavers, especially with respect to the preferred stem diameter (Fryxell & Doucet, 1993; Raffel *et al.*, 2009). To estimate the distance of the inventory plots to the nearest occupied lodge, the length of the shoreline between the lodge and the plot was measured using a georeferenced layer of the park lodges. The lodges were all mapped the year prior to the study, during an extensive inventory of the park realized with a boat and classified as active when fresh mud was observed on it. Distances from a lodge varied between 5 and 500m (median value = 117.5m). This variable was included in the mixed logistic models, both as an independent factor, or in interaction with stem diameter. Neither term was found to be significant, and therefore, the results will not include this variable. Plot number was included as a random effect in order to take the non-independence of the data within a plot into account. The models were checked to verify whether spatial autocorrelation in the residuals was present, based on Euclidian distances between main plots. Spatial autocorrelation was detected only in the residuals of the shrub and sapling models. To correct this issue, the latitude and longitude of each plot was added in these models as a random effect. The effect of the different fixed variables on the odds of stems being consumed was estimated based on odd-ratios (OR), which is defined as the ratio of the probability of being consumed over the probability of not being consumed. If OR = 1, it indicates no effect of the fixed variable on the probability of the stems being consumed. If the OR > 1, the fixed variable increases the odds that stems will be consumed, while an OR < 1 indicates the opposite. The 95% confidence interval (CI) of the OR was used to estimate whether the effect of the fixed variable is significant or not. When the 95% CI included the value of 1, it indicated a non-significant effect of the fixed variable on the odds of stems being consumed.

To determine if a decrease in ash spp. induces a shift in the selection of beavers for other genera (objective 3), it was tested whether the odds of a genus being consumed was affected by ash spp. abundance. Since there was no a priori about selection of items by beavers when the abundance of ash spp. varies, and since there were not enough data to test the effect of the interaction between each genus and each other variable, it was decided to run genus-specific models. Among the genera retained for the second objective, mixed effects logistic regression was run on each genus for which at least three different plots had at least 5 stems consumed. Based on this criterion, four genera of trees and five genera of shrubs or saplings were analyzed. At first, the same fixed and random variables as the models performed for the second objective were included in the models ran for this third objective but the number of ash spp. trees and ash spp. saplings per plot was added as a fixed variable for each stratum. Since the diversity of items present has been shown to influence food selection in other herbivore species, for example, an increase in plant diversity can result in a decrease in the selectivity of items by large herbivores (Champagne *et al.*, 2018; Wang *et al.*, 2011) the Shannon index value of diversity was calculated for each plot and included as a fixed variable. Although the quadratic effect on stem diameter on the probability of shrub and sapling consumption was significant from the analyzes carried out for the second objective, this effect was not significant in the genus-specific models and was therefore not included in any of them. Multicollinearity among independent variables has been tested and detected only between the number of ash saplings and the Shannon index of the trees in the model analyzing the probability of consumption of *Carpinus* and *Acer*. The Shannon index was therefore removed from these models to be able to estimate the effect of the number of ash saplings on the probability of consumption of those two genera, which is the main objective of these analyses. Since no stems of *Ilex* or *Corylus* was larger than 5cm, it was decided not to test the effect of the diameter in these two specific models. All mixed models were run using the glmmTMB package in R 4.1.0.

1.3 Results

1.3.1 Selection for or against a genus by beavers (objective 1)

The selection of trees by beavers in Plaisance National Park was unambiguous since almost all genus were either selected or avoided across the plots as indicated by positive and negative Jacobs index values (Figure 1.3). *Carya* and *Quercus* were the only two tree genera for which beavers did not express a significant selection for or against in any of the plots where they were present (8 and 16 plots, respectively). *Ulmus*, *Acer*, and *Tilia* trees were either not selected at all or significantly selected against, depending on the plot. Of the 21 plots tested, *Ulmus* was significantly selected against in only two of them. *Tilia* was significantly selected against in three of the 14 plots in which the genus was present. Finally, *Acer* was the genus that was significantly selected against the most consistently with nine plots out of 23 in which it was present. The trees of the three remaining genera, *Carpinus*, *Populus*, and ash, were either significantly selected for, or not selected at all. *Carpinus* was significantly selected for in one out of the seven plots where present, while *Populus* was significantly selected for in two out of the 13 plots in which the genus was found. Ash was significantly selected in 15 out of the 24 plots surveyed in this study, making this tree genus the most frequently selected for by beavers at the Plaisance National Park.

Jacobs index values for saplings and shrubs (Figure 1.3) were less straightforward to interpret, as four out of nine genera had positive and negative significant values across plots: *Prunus* (one positive and two negative values out of 14 plots), *Cornus* (three positive and three negative values out of 19 plots), *Tilia* (one positive and one negative value out of 11 plots), and ash (eight positive and one negative values out of 23 plots).

Acer and *Quercus* saplings were significantly selected in one plot out of 13 and 9 plots, respectively. *Carpinus* saplings and *Corylus* shrubs were significantly selected in 3 out of 8 and in 2 out of 7 plots, respectively. *Ilex* was definitively the genus that was significantly selected against the most often, with eight plots with negative Jacobs index values among the 21 plots in which it was present. Ash saplings stand out as the most selected by the beavers in Plaisance National Park, echoing the strong positive selection for ash trees that was found.

The high occurrence of non-significant negative Jacobs index values for both trees and shrubs/saplings is a consequence of these items being available in very small numbers and not consumed. Typically, in these cases, there were around five items or less in the plot, with none of them being consumed.

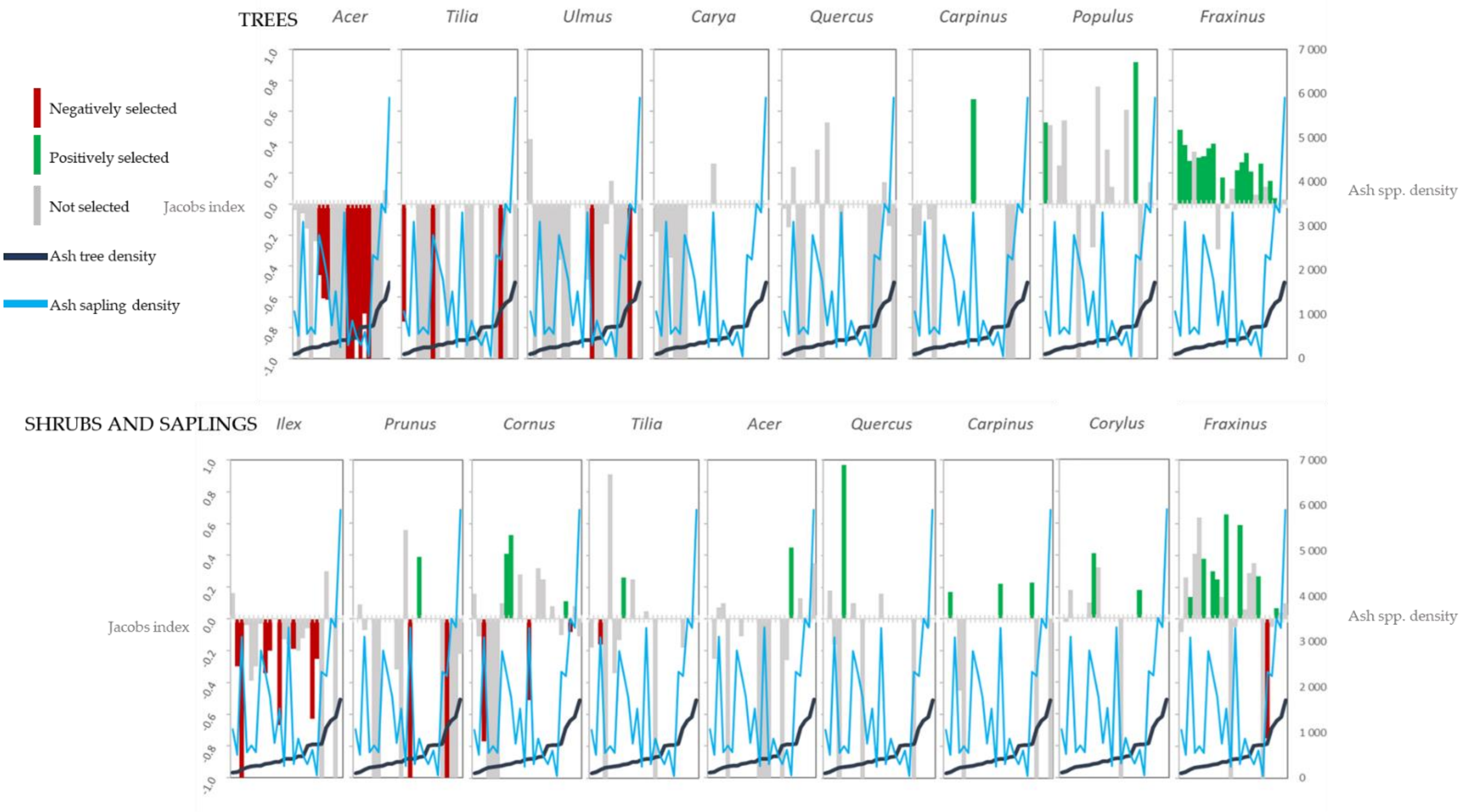

Figure 1.3 Selection of trees (top panel) and saplings and shrubs (bottom panel) by beavers in Plaisance National Park, Quebec, Canada. The Jacobs index was used to establish whether a genus is selected for or against, or not all. A positive Jacobs index value indicates selection of the genera in a given plot (significant values are shown by green vertical bars). A negative Jacobs index value indicates selection against the genus in a given plot (significant values are shown by red vertical bars). Vertical bars in grey indicate Jacobs index values not significantly different from zero and no selection. The black curve represents the density ash spp. trees (per hectare) and the blue curve represents the density of ash spp. saplings (per 0.1 ha).

1.3.2 Beaver selection of non-ash genera relative to ash spp. (Objective 2)

From the sampling conducted in Plaisance National Park, the odds that a stem would be more or less consumed than a stem of ash spp. were either positively or negatively significant for most of the genera tested, both at the tree (Table 1.1) and at the shrub and sapling (Table 1.2) strata. *Populus* trees were significantly and greatly more likely to be consumed than ash spp. trees, and *Carpinus* saplings were significantly more likely to be consumed than ash spp. saplings. *Acer* trees and *Ulmus* (Table 1.1) were significantly less likely to be consumed than the trees of ash spp. *Cornus*, *Ilex* and *Corylus* shrubs, and *Acer* and *Tilia* saplings, were all significantly less likely to be consumed than ash spp. saplings (Table 1.2). The odds of *Quercus* trees or saplings being consumed were not significantly different from ash spp. trees (Table 1.1) or saplings (Table 1.2). The probability of consumption was also not significantly different from that of ash spp. saplings (Table 1.2).

The odds of a stem, be it a tree, a shrub, or a sapling, of being consumed by beavers decreased with increasing distance to the shore (Tables 1.1 and 1.2). The odds that a tree stem would be consumed also decreased also with stem diameter (Table 1.1). The odds of shrubs and saplings being consumed was a quadratic function of stem diameter (Table 1.2).

Table 1.1 The odd-ratios and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for trees being consumed by beavers in Plaisance National Park, depending on their diameter or distance to the shore, and for a genus to be consumed compared to the consumption of ash trees. The model is based on inventories completed in the summer of 2019 in 24 plots 0.15 ha in size. Significant odd-ratios are shown in bold. Consumption of ash spp. is set as the reference class for the genus, so an odd-ratio >1 for a genus indicates a greater odd of being consumed than ash spp., and an odd-ratio < 1 for a genus indicates the opposite.

Variable	**Odd-ratio**	**Confidence interval (95%)**
Diameter	**0.95**	**0.94-0.97**
Distance to the shore	**0.21**	**0.18-0.25**
Acer	**0.07**	**0.05-0.11**
Ulmus	**0.13**	**0.07-0.25**
Quercus	0.64	0.37-1.10
Populus	**18.59**	**8.98-38.48**

Table 1.2 The odd-ratios and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for saplings and shrubs being consumed by beavers in Plaisance National Park, depending on their diameter and squared-diameter values or distance to the shore, and for a genus to be consumed compared to the consumption of ash saplings. The model is based on inventories completed in the summer of 2019 in subplots across 24 plots 0.15 ha in size. Significant odd-ratios are shown in bold. Consumption of ash spp. is set as the reference class for the genus, so an odd-ratio >1 for a genus indicates a greater odd of being consumed than ash spp., and an odd-ratio < 1 for a genus indicates the opposite.

Variable	Odd-ratio	Confidence interval (95%)
Diameter	**1.74**	**1.43-2.11**
Diameter^2	**0.83**	**0.77-0.89**
Distance to the shore	**0.32**	**0.28-0.36**
Ilex	**0.16**	**0.12-0.22**
Acer	**0.41**	**0.25-0.70**
Cornus	**0.43**	**0.32-0.59**
Tilia	**0.45**	**0.25-0.80**
Corylus	**0.53**	**0.31-0.91**
Prunus	0.59	0.32-1.10
Quercus	0.79	0.29-2.17
Carpinus	**1.85**	**1.27-2.68**

1.3.3 Effect of the abundance of ash spp. on the chances of other genera being consumed by beavers (objective 3)

The abundance of ash spp. saplings and trees did not significantly influence the odds that the stems of several other genera would be consumed, and when it did, the increase or decrease was of 5 to 10% for each additional stem per plot (Tables 1.3 and 1.4). Ash sapling abundance increased the odds of *Acer* trees being consumed (ash spp. saplings ranged from 1 to 69 in those plots). The abundance of ash saplings increased the odds of *Carpinus* saplings being consumed (ash spp. saplings ranged from 10 to 116 in those plots) while ash trees decreased these odds (ash spp. trees ranged from 16 to 258 in those plots). Ash sapling abundance increased the odds of *Tilia* saplings of being consumed (ash spp. saplings ranged from 11 to 69 in those plots).

The distance to the shore significantly decreased the odds of a stem being consumed for all tree (Table 1.3) and shrub and sapling (Table 1.4) genera tested when factoring ash spp. abundance in the analyzes. However, this was not the case with the effect of diameter once the abundance of ash spp. was taken into account. The diameter of the tree stem decreased the odds that *Acer* spp. would be significantly consumed, but no such effect was found for *Quercus* and *Populus* spp. (Table 1.3). Sapling stem diameter also did not have a significant effect on the chances that *Acer* and *Populus* saplings were consumed but did significantly increase the odds of *Tilia* saplings consumption (Table 1.4). The diversity of tree genera, based on the Shannon index, greatly and significantly increased the chances that *Acer* trees to be consumed, but did not change the odds for other tree, sapling, or shrub genera tested (Table 1.3 and 1.4). The diversity of the saplings, also based on the Shannon index, had no influence on the genera chances to be consumed.

Table 1.3 The odd-ratios and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for trees of being consumed by beavers at the Plaisance National Park, depending on their diameter, distance to the shore, on the abundance of ash spp. trees and saplings, and on the diversity of trees and saplings, based on the Shannon index. The model is based on inventories completed in the summer of 2019 in 24 plots 0.15 ha in size. Significant odd-ratios are shown in bold. A significant odd-ratio >1 indicate a positive effect of the variable on the chances that a stem is consumed, while a significant odd-ratio <1 indicate the opposite.

Genus	***Acer***	***Quercus***	***Populus***
Intercept	**0.01 [2.11e-05-0.20]**	2009.20 [0.05-8.39e+07]	38.16 [0.03-4.87e+04]
Diameter	**0.96 [0.93-0.99]**	0.95 [0.90-1.01]	0.98 [0.94-1.02]
Distance to the shore	**0.29 [0.16-0.51]**	**0.47 [0.30-0.75]**	**0.43 [0.25-0.74]**
Abundance of ash trees	1.00 [0.99-1.01]	0.98 [0.95-1.01]	1.00 [0.98-1.02]
Abundance of ash saplings	**1.05 [1.03-1.07]**	1.03 [0.99-1.08]	1.00 [0.94-1.06]
Shannon index for trees	**7.07 [1.06-47.19]**	0.08 [0.00-6.81]	1.56 [0.11-21.52]
Shannon index for saplings	1.62 [0.65-4.04]	0.45 [0.04-5.21]	0.44 [0.08-2.49]

Table 1.4 The odd-ratios and corresponding 95% confidence intervals estimated from a mixed-effects logistic regression for saplings or shrubs of being consumed by beavers in Plaisance National Park, depending on their diameter, distance to the shore, on the abundance of ash spp. trees and saplings, and on the diversity of trees and saplings, based on the Shannon index. The model is based on inventories completed in the summer of 2019 in 24 plots 0.15 ha in size. Significant odd-ratios are shown in bold. A significant odd-ratio >1 indicate a positive effect of the variable on the chances that a stem is con-sumed, while a significant odd-ratio <1 indicate the opposite. The diameter was not tested for *Ilex* and *Corylus* since almost all the items available for these genera were in the lowest diameter class. The Shannon index for the trees was not tested for *Acer* and *Carpinus* due to the presence of multicollinearity.

Genus	***Acer***	***Carpinus***	***Tilia***	***Ilex***	***Corylus***
Intercept	0.19 [0.01-31.84]	1.69 [9.32e-04-3052.54]	1.02 [5.41e-07-1.91e+06]	0.21 [8.65e-04-53.11]	422.36 [0.13-1.32e+06]
Diameter	1.15 [0.86-1.54]	0.81 [0.65-1.01]	**1.49 [1.04-2.13]**	*Not tested*	*Not tested*
Distance to the shore	**0.69 [0.48-0.99]**	**0.77 [0.67-0.88]**	**0.56 [0.34-0.93]**	**0.62 [0.56-0.69]**	**0.74 [0.65-0.84]**
Abundance of ash trees	0.99 [0.97-1.02]	**0.95 [0.91-0.99]**	0.99 [0.96-1.02]	1.00 [0.98-1.02]	0.98 [0.96-1.01]
Abundance of ash saplings	1.03 [0.97-1.08]	**1.10 [1.01-1.20]**	**1.08 [1.02-1.15]**	1.04 [0.99-1.08]	1.03 [0.98-1.09]
Shannon index for trees	*Not tested*	*Not tested*	3.10 [0.01-879.43]	1.96 [0.12-32.16]	0.29 [0.00-18.26]
Shannon index for saplings	1.98 [0.14-28.03]	1.32 [0.02-77.36]	0.16 [0.00-5.38]	0.72 [0.08-6.76]	0.18 [0.01-4.07]

1.4 Discussion

This study clearly shown that ash spp. was a large part of the woody diet of the beaver in a riparian temperate forest. Ash trees accounted for 58% of the total amount of trees in the community but represented more than 80% of the consumed trees by the beaver. Ash saplings represented a smaller part of both the available and consumed stems, but still accounted for 20% of the total amount of saplings and shrubs (770 over 3840) and 29% of the consumed saplings and shrubs (412 over 1413), meaning that 54% of the ash saplings were consumed (412 over 770). More specifically, we found that the tree genus that were most frequently selected by the beaver in the riparian temperate forests of Plaisance National Park was ash spp. (63% of the time the genus was present in the study plots), and that the sapling genera most frequently selected by beavers were also ash spp. and *Carpinus* (at least one-third of the time the genera were present in the study plots). We also found that *Carpinus* saplings were also more likely to be consumed by the beaver than ash spp. Saplings, and *Populus* trees were more likely to be consumed than ash spp. Trees. Finally, the abundance of ash spp. trees and saplings had mixed effects on the likelihood of stems of other genera of being consumed: *Carpinus* saplings were more likely to be consumed with a decrease in the abundance of ash spp. trees, while *Acer* trees and *Carpinus* and *Tilia* saplings were less likely to be consumed with the decrease in the abundance of ash spp. The odds of *Quercus* and *Populus* trees and of *Ilex* and *Corylus* shrubs, of being consumed were not influenced by the densities of trees or shrubs of ash spp.

Ash spp. are not only largely consumed by the beaver but are highly selected for and across a large range of ash sapling and tree densities (Objective 1). In only one instance, ash spp. were selected against, a result that could be attributed to the high number of *Carpinus* saplings available in this particular plot where they represented 85% of the total consumed stems. Indeed, *Carpinus* saplings were also found to be 85% more likely to be consumed than saplings from ash spp. (Objective 2). *Populus* was the only genus of trees that was significantly more likely to be consumed than trees of ash spp. Although *Populus* trees were positively selected in only two of the 13 plots where the genus was present (Objective 1), *Populus* trees were more than 18 times more likely to be consumed than ash spp trees (Objective 2).

The distinction between genus selected for and selected against is very clear for the trees, with three genera selected for (*Carpinus*, *Populus* and *Fraxinus*) and three genera selected against (*Ulmus*, *Tilia*, and *Acer*). The distinction between genera selected for and selected against is not as clear for saplings and shrubs as it was for the trees, especially for some genera that are selected for and selected against in a similar number of plots (Objective 1). However, ash spp. still remains the genus that is positively selected in the highest number of plots at the sapling stage, indicating that this preference for ash spp. is not dependent on stem height.

The varying abundance and dominance of ash spp. across the riparian forest stands in Plaisance National Park allowed to observe how the food items by beavers would change with this variable (objective 3). The abundance of ash spp. trees had a negative effect on the odds that *Carpinus* saplings would be consumed (ie, OR = 0.95 which indicates a 5% reduction for the odds of *Carpinus* saplings of being consumed when the abundance of ash spp. trees increased by one stem at the plot level). On the opposite, the abundance of ash ssp. saplings had a positive effect on the chances of *Acer* trees to be consumed (a 5% increase for each additional stem at the plot level). Each increase of one ash spp. sapling at the plot-level also increased by 10% and 8%, respectively, the chances of *Carpinus* and *Tilia* saplings being consumed. It is not possible to rule out, in these cases, the possibility that ash spp. caused an indirect negative impact on other genera (apparent competition) (Rand, 2003). Indeed, it cannot be excluded that as the abundance of ash spp. saplings increased, the plots became more attractive for beavers, increasing the chances that other genera would be consumed as well. In any case, the plot-level diversity of trees also increased the chances of *Acer* trees to be consumed. *Acer* trees may therefore still be targeted by beavers in highly diverse stands when ash spp. will disappear because of the EAB, since it appears that the Shannon index for the trees had a great impact on *Acer* chances of being consumed. It is unlikely that the abundance of other genera could have positively or largely influenced the patterns of consumption that were observed in the park, mainly because ash spp. was the only genus that was consumed systematically across the plots at both the sapling and tree levels. When feeding occurred in a majority of plots for other genera, their stems were generally not selected, or selected against.

One genus that was present in a majority of plots, at least at the tree level, and was found to have the same likelihood of being consumed as ash spp. trees, was *Quercus*. This could potentially mean that when available, it could be a genus that will replace ash spp. in the beaver’s diet. This would be consistent with Raffel *et al.*, (2009) who found that *Quercus* was highly selected by beavers. However, in the case of Plaisance National Park, the relatively low abundance of *Quercus* will probably disqualify it from replacing ash spp. as a staple for feeding resources for beavers. More generally, northern red oak (*Quercus rubra* L.) and bur oak (*Quercus macrocarpa* Michx.), the two most abundant species of oaks present in the park, and the most frequent oak species in northern temperate woods, are not abundant in poorly drained soil. In riparian forests of the Canadian Great Lakes and St. Lawrence Lowlands, they are thus limited to mounds. However, in some studies, *Q. rubra* can be described as abundant in some riparian forests stands (Nisbet *et al.*, 2015; Raffel *et al.*, 2009). In such cases, and if ash spp. was also abundant in those stands, it could to some extent that *Q.rubra* replace ash spp. as a main food resource for beavers.

It is difficult from our results to generate precise predictions about the future composition of riparian temperate forests, mainly because ash spp. stands out as the main food item for beavers and no other genera can be considered to be an equivalent alternative, which is likely a consequence of these ecosystems (1) being diverse, (2) not abundant with more boreal dominant preferred items, such as *Populus* and *Salix*, and (3) not abundant with selected more meridional items such as *Carpinus* which are selected by beavers. Since ash spp. have a bleak future because of the EAB, the dynamics in these riparian temperate deciduous forests has now more to do with the response of beavers to this new disturbance agent on ash trees as food resources than with the dynamics generated by beavers on forest cover tree composition in those ecosystems.

In regard of the future of ash tree species, it seems that until the current seed bank and seed production are severely reduced, seedlings may remain abundant, although less so in lowland forests than in upland forests (Kashian & Witter, 2011). Ash could also be maintained from stump sprouts; however, the emerald ash borer was shown to be capable of recolonizing stems as small as 2 cm in diameter (Aubin *et al.*, 2015). Given that the most selected stem size by beavers in Plaisance National Park is in the 3.1-5 cm size class, both the beavers and the EABs will be in competition for the same resource, although it is not yet known what the colonization rate by the insect would be in relation to stem size if ash is maintained as saplings or sprouts. Because the beavers in the park expressed a stronger selection for intermediate size saplings, it is also difficult to predict whether ash saplings consumption rate would be a Type II (Fryxell *et al.*, 1994) or a Type III (Fryxell & Doucet, 1993) functional response when the resource is only present as saplings or resprouts. Despite the ash saplings' density gradient in this study (51 to 5,908 stems/ha), it was not possible to fit any type of functional response to the data. Since ash was not the only resource available to beavers when ash was at low densities, it may not be possible to clearly extract the functional response expressed by beavers. Providing projections into the future, would require realistic manipulative experiments such as cafeteria experiments (Durben *et al.*, 2021; Fryxell & Doucet, 1993; Kimball & Perry, 2008). This study is not sufficient to draw conclusions on the relative importance of saplings and trees in beavers' diet. The fact that the quadratic effect on the diameter was significant only for saplings implies that the preferred diameter for beavers is around 3.1-5 cm (across all the diameter spectrum, from saplings to trees). However, all stems cannot be considered equal, and the fact that trees are less likely to be cut down than saplings does not necessarily mean that they are less important in the beaver's diet, since the potential biomass that can be harvested on large trees is likely greater than what can be harvested on small saplings.

Beavers are well known to have the ability to shape the composition of riparian forests (e.g., Barnes & Dibble, 1988; Johnston & Naiman, 1990). In the case of Plaisance National Park, and more generally, the riparian temperate forest, it is considered that tree and shrub diversity could be the key to mitigate the potential damage that beavers could do to the forest cover. Being a picky generalist, it is possible that its diet selection will change depending on the most available plant genera – if not deterred to feed on it, allowing them to thrive in some areas. It is also important to note that despite the beavers being able to alter forest composition, their impact on the forest remains limited to the first meters from the shoreline.

Finally, to determine whether the intensity of the pressure caused by the beavers foraging activity will remain the same over time, it could be relevant to determine if ash stems increase the quality of the environment to a level which in turn affects their population densities. It has already been shown that the preferred food items for beavers is tied to changes in local populations dynamics. For example, how willow species recover rapidly after being browsed by beavers could have fueled the increase in the number of beaver colonies in Yellowstone National Park (Smith & Tyers, 2012). Furthermore, the density of *Populus* has already been shown to influence the number of kits per colony (Smith, 1997). Because of the importance of ash in the beaver's diet, it is plausible that ash in the temperate deciduous forest may also influence the size of beaver populations. If this is the case, the disappearance of ash from riparian temperate forests could likely result in a general decrease in beaver density. Investigations are underway to determine whether this potential decrease will occur through an expansion of territory size or through a decrease in the size of the colony group. Regardless of these two alternatives, a decrease in the density of beavers would necessarily reduce the browsing pressure on trees, saplings, and shrubs on the riverbank, reducing damage to the riparian forest.

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1.5 References

Aubin, I., Cardou, F., Ryall, K., Kreutzweiser, D., & Scarr, T. (2015). Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. The Forestry Chronicle, 91(3), 291–298.

Barnes, W. J., & Dibble, E. (1988). The effects of beaver in riverbank forest succession. Canadian Journal of Botany, 66, 40–44. https://doi.org/10.1139/b88-005

Busher, P. E. (1996). Food Caching Behavior of Beavers (Castor canadensis): Selection and Use of Woody Species. The American Midland Naturalist, 135(2), 343–348. http://www.jstor.orgURL:http://www.jstor.org/stable/2426717

Champagne, E., Dumont, A., Tremblay, J. P., & Côté, S. D. (2018). Forage diversity, type and abundance influence winter resource selection by white-tailed deer. Journal of Vegetation Science, 29(4), 619–628. https://doi.org/10.1111/jvs.12643

Cook, J. E. (2005). Torrey Botanical Society Vegetation Changes in a Central Wisconsin Floodplain from Pre-Settlement to the Mid-21st Century. The Journal of the Torrey Botanical Society, 132(3), 492–504. http://www.jstor.orgURL:http://www.jstor.org/stable/20063788

Deardorff, J. L., & Gorchov, D. L. (2021). Beavers cut, but do not prefer, an invasive shrub, Amur honeysuckle (Lonicera maackii). Biological Invasions, 23(1), 193–204. https://doi.org/10.1007/s10530-020-02365-8

Donkor, N. T., & Fryxell, J. M. (2000). Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (Castor canadensis) foraging and edaphic factors. Plant Ecology, 148, 1–12.

Durben, R. M., Walker, F. M., Holeski, L., Keith, A. R., Kovacs, Z., Hurteau, S. R., Lindroth, R. L., Shuster, S. M., & Whitham, T. G. (2021). Beavers, bugs and chemistry: A mammalian herbivore changes chemistry composition and arthropod communities in foundation tree species. Forests, 12(7). https://doi.org/10.3390/f12070877

Engelken, P. J., & McCullough, D. G. (2020). Riparian forest conditions along three northern Michigan rivers following emerald ash borer invasion. Canadian Journal of Forest Research, 50(8), 800–810. https://doi.org/10.1139/cjfr-2019-0387

Ewel, K. C., Cressa, C., Kneib, R. T., Lake, P. S., Levin, L. A., Palmer, M. A., Snelgrove, P., & Wall, D. H. (2001). Managing critical transition zones. Ecosystems, 4(5), 452–460. https://doi.org/10.1007/s10021-001-0106-0

Forio, M. A. E., De Troyer, N., Lock, K., Witing, F., Baert, L., De Saeyer, N., Rîșnoveanu, G., Popescu, C., Burdon, F. J., Kupilas, B., Friberg, N., Boets, P., Volk, M., McKie, B. G., & Goethals, P. (2020). Small patches of riparian woody vegetation enhance biodiversity of invertebrates. Water (Switzerland), 12(11), 1–21. https://doi.org/10.3390/w12113070

Fryxell, J. M., & Doucet, C. M. (1993). Diet Choice and the Funcional Response of Beavers. Ecology, 74(5), 1297–1306.

Fryxell, J. M., Vamosi, ; S M, Walton, R. A., & Doucet, ; C M. (1994). Retention Time and the Functional Response of Beavers. Oikos, 71(2), 207–214.

Gandhi, K. J. K., & Herms, D. A. (2010). North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien Emerald ash borer. Biological Invasions, 12(6), 1839–1846. https://doi.org/10.1007/s10530-009-9594-1

Gregory, S. v, Swanson, F. J., McKee, W. A., & Cummins, K. W. (1991). An Ecosystem Perspective of Riparian Zones. BioScience, 41(8), 540–551. http://www.jstor.org/action/showPublisher?publisherCode=aibs.

Grinde, A. R., Youngquist, M. B., Slesak, R. A., Kolbe, S. R., Bednar, J. D., Palik, B. J., & D’Amato, A. W. (2022). Potential impacts of emerald ash borer and adaptation strategies on wildlife communities in black ash wetlands. Ecological Applications. https://doi.org/10.1002/eap.2567

Haack, R. A., Jendek Eduard, Liu Houping, Marchant Kenneth R., Petrice Toby R., Poland Therese M., & Ye Hui. (2002). The Emerald Ash Borer: A New Exotic Pest in North America. Michigan Entomological Society, 47(3 and 4), 1–5.

Hall, J. G. (1960). Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology, 41(3), 484–494. https://doi.org/10.2307/1933323

https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/black-ash-2018.html. (2022, June 15). https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/black-ash-2018.html

Hunter, M. L., Acuña, V., Bauer, D. M., Bell, K. P., Calhoun, A. J. K., Felipe-Lucia, M. R., Fitzsimons, J. A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C. J., Medellin, R. A., Nelson, E. J., & Poschlod, P. (2017). Conserving small natural features with large ecological roles: A synthetic overview. Biological Conservation, 211, 88–95. https://doi.org/10.1016/j.biocon.2016.12.020

Jacobs, J. (1974). Quantitative Measurement of Food Selection A Modification of the Forage Ratio and Ivlev's Electivity Index. Oecologia, 14, 413–417.

Johnston, C. A., & Naiman, R. J. (1990). Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research, 20, 1036–1043. https://doi.org/10.1139/x90-138

Kashian, D. M., & Witter, J. A. (2011). Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. Forest Ecology and Management, 261(3), 480–488. https://doi.org/10.1016/j.foreco.2010.10.033

Kimball, B. A., & Perry, K. R. (2008). Manipulating beaver (Castor canadensis) feeding responses to invasive tamarisk (Tamarix spp.). Journal of Chemical Ecology, 34(8), 1050–1056. https://doi.org/10.1007/s10886-008-9496-1

King, S. L., & Antrobus, T. J. (2005). Relationships between gap makers and gap fillers in an Arkansas floodplain forest. Journal of Vegetation Science, 16, 471–480.

Knight, K. S., Brown, J. P., & Long, R. P. (2013). Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (Agrilus planipennis). Biological Invasions, 15(2), 371–383. https://doi.org/10.1007/s10530-012-0292-z

Lafond, R., Leblanc, Y., Pilon, C., & Société de la faune et des parcs du Québec. Direction du développement de la faune. (2003). Bilan du plan d'inventaire aérien des colonies de castors au Québec (1989-1994). Société de la faune et des parcs du Québec, Direction du développement de la faune.

MacFarlane, D. W., & Meyer, S. P. (2005). Characteristics and distribution of potential ash tree hosts for emerald ash borer. Forest Ecology and Management, 213, 15–24. https://doi.org/10.1016/j.foreco.2005.03.013

Maisonneuve, C., & Rioux, S. (2001). Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Québec. Ecosystems and Environment, 83, 165–175.

Major, M., Gosselin, Jocelyn., Landry, Yves., Québec (Province). Direction des inventaires forestiers., & Québec (Province). Ministère des ressources naturelles et de la faune. Direction des communications. (2012). Guide de reconnaissance des types écologiques. Région écologique 1a : plaine du bas Outaouais et de l'archipel de Montréal. Ministère des ressources naturelles et de la faune, Forêt Québec, Direction des inventaires forestiers.

Martell, K. A., Foote, A. L., & Cumming, S. G. (2006). Riparian disturbance due to beavers (Castor canadensis) in Alberta's boreal mixedwood forests: Implications for forest management. Ecoscience, 13(2), 164–171. https://doi.org/10.2980/i1195-6860-13-2-164.1

Müller-Schwarze, D., Schulte, B. A., Sun, L., Müller-Schwarze, A., & Müller-Schwarze, , Christine. (1994). Red Maple (*Acer* Rubrum) Inhibits Feeding By Beaver (Castor canadensis). Journal of Chemical Ecology, 20(8).

Musolin, D. L., Selikhovkin, A. v., Peregudova, E. Y., Popovichev, B. G., Mandelshtam, M. Y., Baranchikov, Y. N., & Vasaitis, R. (2021). North-westward expansion of the invasive range of emerald ash borer, agrilus planipennis fairmaire (Coleoptera: Buprestidae) towards the EU: From Moscow to Saint Petersburg. Forests, 12(4), 502. https://doi.org/10.3390/f12040502

Naiman, R. J., & Decamps, H. (1997). The Ecology Of Interfaces-Riparian Zones. Annual Review of Ecology and Systematics, 621–658.

Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American Streams by Beaver. BioScience, 38(11), 753–762. http://www.jstor.orgURL:http://www.jstor.org/stable/1310784Accessed:18/06/200814:47

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor Canadensis). Ecology, 67(5), 1254–1269.

Nisbet, D., Kreutzweiser, D., Sibley, P., & Scarr, T. (2015). Ecological risks posed by emerald ash borer to riparian forest habitats: A review and problem formulation with management implications. Forest Ecology and Management, 358, 165–173. https://doi.org/10.1016/j.foreco.2015.08.030

Nummi, P., Liao, W., Huet, O., Scarpulla, E., & Sundell, J. (2019). The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. Global Ecology and Conservation, 20. https://doi.org/10.1016/j.gecco.2019.e00701

Paine, L. K., & Ribic, C. A. (2002). Comparison of riparian plant communities under four land management systems in southwestern Wisconsin. Ecosystems and Environment, 92, 93–105.

Poland, T. M., Chen, Y., Koch, J., & Pureswaran, D. (2015). Review of the emerald ash borer (Coleoptera: Buprestidae), life history, mating behaviours, host plant selection, and host resistance. Canadian Entomologist, 147, 252–262. https://doi.org/10.4039/tce.2015.4

Raffel, T. R., Smith, N., Cortright, C., & Gatz, A. J. (2009). Central Place Foraging by Beavers (Castor canadensis) in a Complex Lake Habitat. The American Midland Naturalist, 162(1), 62–73. http://www.jstor.orgURL:http://www.jstor.org/stable/25602298http://www.jstor.org/stable/25602298?seq=1&cid=pdf-reference#references_tab_contents

Rand, T. A. (2003). Herbivore-Mediated Apparent Competition Between Two salt Marsh Forbs. Ecology, 84(6), 1517–1526.

Rosell, F., Bozsér, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. Mammal Rev, 35(4), 248–276.

Rossell, R. C. J., Arico, S., Clarke, D. H., Horton, J. L., Rhode Ward, J., & Patch, S. C. (2014). Forage Selection of Native and Nonnative Woody Plants by Beaver in a Rare-Shrub Community in the Appalachian Mountains of North Carolina. Southeastern Naturalist, 13(4), 649–662.

Smith, D. W. (1997). Dispersal strategies and cooperative breeding in beavers. University of Nevada.

Smith, D. W., & Tyers, D. B. (2012). The history and current status and distribution of beavers in Yellowstone National Park. Northwest Science, 86(4), 276–288. https://doi.org/10.3955/046.086.0404

Stoffyn-Egli, P., & Willison, J. H. M. (2011). Including wildlife habitat in the definition of riparian areas: The beaver (Castor canadensis) as an umbrella species for riparian obligate animals. In

Environmental Reviews (Vol. 19, Issue 1, pp. 479–493). National Research Council of Canada. https://doi.org/10.1139/a11-019

Vorel, A., Válková, L., Hamšíková, L., Maloň, J., & Korbelová, J. (2015). Beaver foraging behaviour: Seasonal foraging specialization by a choosy generalist herbivore. Behavioral Ecology and Sociobiology, 69(7), 1221–1235. https://doi.org/10.1007/s00265-015-1936-7

Wang, L., Wang, D., Liu, J., Huang, Y., & Hodgkinson, K. C. (2011). Diet selection variation of a large herbivore in a feeding experiment with increasing species numbers and different plant functional group combinations. Acta Oecologica, 37(3), 263–268. https://doi.org/10.1016/j.actao.2011.02.010

www.fs.fed.us. (2022, June 15).

Zavyalov, N. A. (2014). Beavers (Castor fiber and Castor canadensis), the founders of habitats and phytophages. Biology Bulletin Reviews, 4(2), 157–180. https://doi.org/10.1134/s207908641402008x

CHAPITRE 2

RESOURCE AVAILABILITY AFFECTS GROUP SIZE BUT NOT TERRITORY SIZE IN A TERRITORIAL SOCIAL SPECIES, THE AMERICAN BEAVER (*CASTOR CANADENSIS*)

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RÉSUMÉ

La densité des ressources est un facteur important qui détermine la qualité de l'habitat et la densité des espèces animales. Pour une espèce sociale territoriale, la densité de sa population peut être déterminée par la taille du groupe, la taille du territoire ou les deux. Dans cette étude, nous avons investigué par quel mécanisme la densité des ressources alimentaires influence les populations de castors d'Amérique (*Castor canadensis*) dans des forêts tempérées à composition hétérogène en zone riparienne, mais dominées à divers degrés par les frênes (*Fraxinus* spp.). En 2021, nous avons capturé 25 castors de différentes colonies dans le parc national de Plaisance (Québec, Canada) et équipé chaque castor d'une balise GPS pour suivre leurs déplacements et délimiter leurs territoires respectifs. Nous avons déterminé la taille des groupes à l'aide d'un drone. La densité de diverses ressources alimentaires a été mesurée et incluse dans nos modèles linéaires généralisés afin de déterminer les ressources affectant la taille du groupe ou du territoire. Nous avons observé que la taille du groupe était positivement liée à la densité des frênes, mais nous n'avons pas pu démontrer de relation entre la taille du territoire et la densité des ressources. Dans le contexte de l'invasion en cours de l'agrile du frêne (*Agrilus planipennis*) nous prévoyons que les populations de castors seront affectées négativement par la disparition des frênes, en particulier dans les forêts riveraines dominées par les frênes. Nos résultats suggèrent que le coût de la défense du territoire est probablement compensé par certains mécanismes tels que les soins alloparentaux ou l'effet du cher ennemi. Les mécanismes potentiels devraient être étudiés de manière plus approfondie afin de déterminer lesquels d’entre eux sont impliqués dans la réduction des coûts de la territorialité.

Mots-clés: Agrile du Frêne, Castor, Disponibilité des ressources alimentaires, Forêt riparienne, Frêne, Taille du groupe, Superficie du territoire

ABSTRACT

Food density is an important driver of habitat quality and animal density. For a territorial social species, population density can be determined by group size, territory size, or both. In this study, we investigated by which mechanisms food resources density affects American beaver (*Castor canadensis*) populations in temperate riparian forest habitats dominated by ash (*Fraxinus* spp.) in diversified stands. In 2021, we captured 25 beavers from different colonies in Plaisance National Park (Quebec, Canada) and equipped them with a GPS tag to track their movements and delimit their respective territories. We determined group size using aerial imagery obtained from a drone. The density of various food resources was measured and included in generalized linear models to determine how resources affect either group size or territory size. We observed that group size was positively related to ash tree density but we did not find any relationship between territory size and resource density. In the context of the ongoing invasion of the emerald ash borer (*Agrilus planipennis*) and the large distribution area of ash species in North America, we predict that beaver populations will be negatively affected by the massive death of ash trees, especially in ash-dominated riparian forests. Our results suggest that the cost of territorial defence is likely compensated by the benefit of securing territories where resource density is high and which support larger groups of individuals, an unexpected observation for such a territorial species. However, other mechanisms such as alloparental care or the dear enemy effect may be involved to mitigate the cost of territoriality and require further investigation.

Keywords: Ash spp., Beaver, Emerald ash borer, Group size, Resource availability, Riparian forest, Territory size

2.1 Introduction

Understanding how animal population density varies over time and space is a recurring question in fundamental and applied ecology. For territorial social species, population density can be expressed as the average group size, *i.e.*, the average number of individuals in a territory, divided by the average territory size (Mosser *et al.*, 2009); thus, density can be altered by variations in either the size of the territory, group, or both (Figure 2.1). Resource availability, one of the primary components of habitat quality (Johnson 2007), may influence territory (Kittle *et al.*, 2015) and group size (Kruuk & Parish, 1982). However, the effect of habitat quality on the density of territorial social species has not been fully addressed in terms of the mechanism involved: territory or group size (Kittle *et al.*, 2015).

Habitat quality can negatively affect territory size. As first described by Huxley (1934), territories can be viewed as elastic discs that can be compressed to a certain size to set the maximum density of individuals for a given habitat. The territory will thus be at a size that balances the need to maximize the amount of resources while minimizing the cost of their defense, a strategy also labelled as economic defendability (Brown, 1964). This idea implies an inverse relationship between habitat quality and territory size, a concept demonstrated for several species (e.g., Patterson & Messier, 2001). If territories are smaller in rich habitats, but group size is unaffected, more territories will fit within an area and population density will increase (Mechanism 1, Figure 2.1). Alternatively, group size, which reflects the fitness of species that live in groups comprising a reproductive couple and their offspring, may increase with resource availability without affecting territory size. This theory is consistent with observations that reproductive success can result directly from resource quantity or quality (Cury *et al.*, 2011). It is also consistent with the resource dispersion hypothesis, originally proposed to describe group-living in social carnivores and has since been widely invoked for several species (Macdonald, 1983 Johnson *et al.*, 2002). Since its inception, this hypothesis has also been used to understand sociality in multiple taxa, including herbivores (Herrera *et al.*, 2011). Two of its predictions are 1) group size is correlated with resource quality; and 2) territory and group size are independent (Johnson *et al.*, 2002; Robertson *et al.*, 2015). Evidently, if habitat quality positively influences average group size, the population density of an area will increase (Mechanism 2, Figure 2.1).

Finally, the availability of resources may influence both group and territory size. For instance, the ideal despotic distribution hypothesis (Fretwell & Lucas, 1969) postulates that territory size will decrease and fitness will increase when resource availability increases (Calsbeek & Sinervo, 2002). For territorial species living in monogamous family units, group size and fitness are closely related. In such cases, habitat quality can influence population density through both group and territory size (Mechanism 3, Figure 2.1).

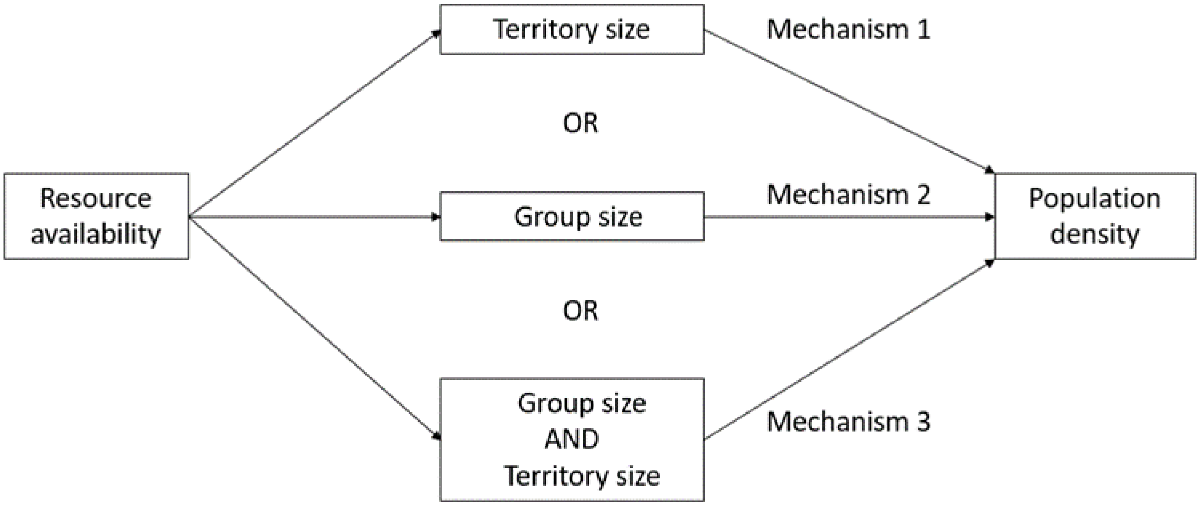

Figure 2.1 Possible mechanisms leading resource availability to affect population density of territorial social species, by a modification of either group or territory size, or both.

Understanding the mechanisms by which resource availability affects the population density of a given territorial social species is vital for identifying ecological thresholds (Johnson, 2013). The most important variable can be identified to help for conservation and population management purposes or in the event of large and intense disturbances that modify resource quality or quantity.

American beaver (*Castor canadensis,* Kuhl) is a territorial rodent species (DeStefano *et al.* 2006; Mayer *et al.* 2020a; 2020b) that lives in family groups consisting of a breeding pair and their offspring, usually the kits and the yearlings (Payne, 1982). The population density of American beaver is positively related to the availability of aquatic vegetation, which can make up most of a beaver's diet (Milligan & Humphries, 2010), or its preferred tree species (Bergman *et al.*, 2018; Fryxell, 2001; Smith, 1997; Smith & Tyers, 2012). However, the mechanism by which population density varies with resource availability is not certain, specifically whether the effect occurs through territory or group size. Some studies have shown that greater resource availability favours an increase in the number of beaver family units in an area (Bergman *et al.*, 2018; Smith & Tyers, 2012), whereas other research found an increased group size (Fryxell, 2001; Smith, 1997). Determining the role of resource availability on beaver population density is critical, as it can help forecast the influence of resource availability on tree species composition trajectories of riparian forests. Indeed, through its selective feeding, the beaver favors the tree species it avoids and affects those it selects for forage (Johnston & Naiman, 1990). Poplars (*Populus* spp.) and willows (*Salix* spp.) are known to influence positively beaver populations, either by increasing their fitness or by increasing the colony density (Smith, 1997; Smith & Tyers, 2012). However, when these two genera are absent or scarce, other trees and shrubs genera may be highly selected, such as ash trees (*Fraxinus* spp.), which can sometimes be the staple food resource of beavers (Barnes & Dibble, 1988; Rosner *et al.*, 2022). It is unknown whether the abundance of ash trees can influence the density of beaver populations in the same manner as other preferred resources, and, if so, whether this influence occurs through variations in group size, territory size or both. This question is of particular interest because the current invasion of emerald ash borer (*Agrilus planipennis* Fairmaire) threatens the future of ash-dominated riparian forests (Engelken and McCullough 2020), which could therefore negatively affect beaver populations and ultimately vegetation dynamics of riparian forests.

Our study aim to determine whether resource availability and, in particular, ash tree availability has the potential to influence beaver populations through territory size (Mechanism 1), group size (Mechanism 2), or both (Mechanism 3). As resource density represents a good indicator of habitat quality, we test its effect on both group and territory sizes. If Mechanism 1 dominates, we predict a negative relationship between territory size and resource density (Prediction 1.1), and group size should be independent of resource density, thus no relationship should be detected (Prediction 1.2). On the other hand, if Mechanism 2 dominates, territory size should be independent of resource density, thus no relationship should be observed (Prediction 2.1), but group size should increase with resource density (Prediction 2.2). Finally, if the density of beaver populations is mediated though changes in both group and territory sizes, then we should observe that territory size decreases with resource density (Prediction 1.1) and that group size increases with resource density (Prediction 2.2).

2.2 Materials & methods

2.2.1 Study site

Our study was carried out in the riparian temperate forest of Plaisance National Park, Quebec, Canada (Figure 2.2). This 28 km^2 park contains many islands and peninsulas. Overall, the forest basal area comprises 25% ash (*Fraxinus* spp.) and 25% maple (*Acer* spp.), with the remaining 50% a very heterogeneous mix of species (e.g., *Quercus* spp., *Tilia* spp., *Populus* spp., and *Ulmus* spp.). However, the respective densities of maple and ash vary from scattered to dominant. The park also supports one of the highest densities of beavers in Quebec. For a more detailed description of the study site, see Rosner *et al.* (2022).

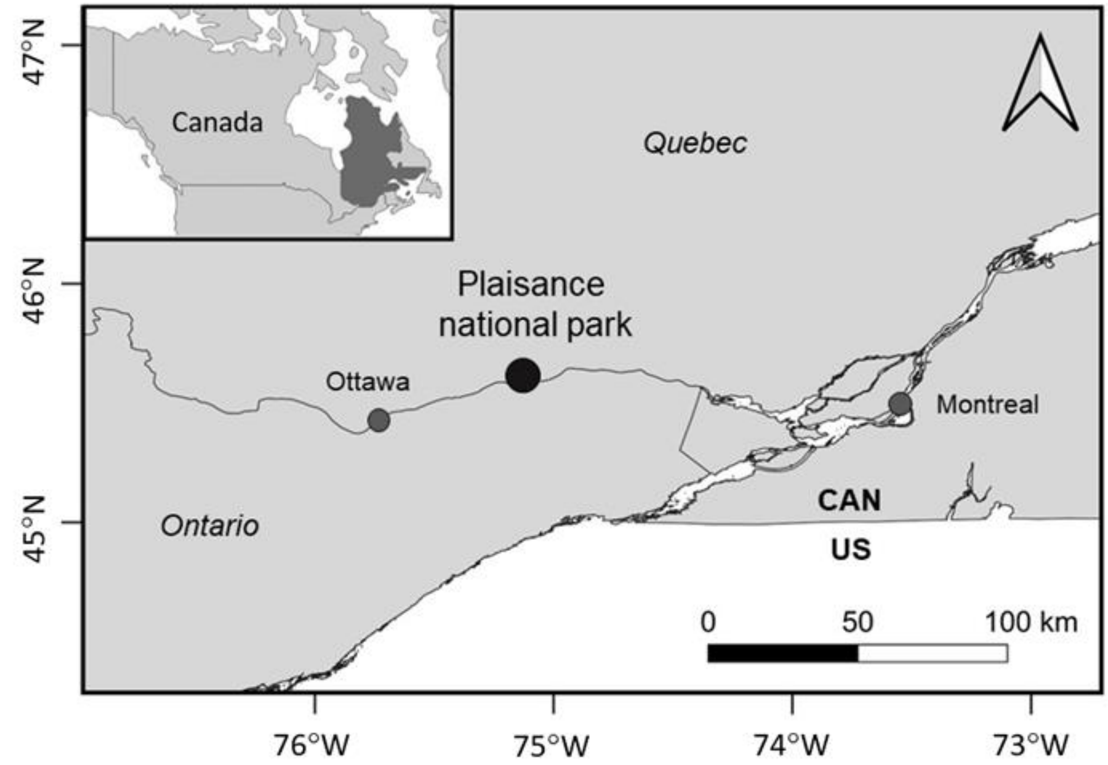

Figure 2.2 Map showing the location of Plaisance National Park, Quebec (Canada).

2.2.2 Beaver trapping

Between April 6 and June 4, 2021, when the water bodies were ice-free, we captured 25 beavers with live traps (KORO ‘Klam’ Live and Hancock Live traps, Wildlife Control Supplies, Suffield, CT, USA) positioned at the land–water interface. The traps were set at dusk and checked at dawn, less than 12 h later. The traps were baited with fresh twigs of trembling aspen (*Populus tremuloides*) and castoreum provided by a local trapper. Beavers were weighed and were considered adults if they weighed more than 15 kg (Aleksiuk & Cowan, 1969). Adult beavers were transferred to a restraint bag to facilitate their handling. All adult beavers were fitted with a GPS tracker with a cellular network transfer capability (Oyster 2 - 4G, Digital Matter; WestCoast GPS, North Vancouver, BC, Canada). GPS trackers were set to record the position of the beavers every 15 minutes between 18h00 and 4h00 from April 6 to June 17. Although already water resistant (rated IP-67), the GPS trackers were covered with two layers of a polyurethane coating (SikaTack DRIVE

60min, Vanfax, Laval, QC, Canada). A mesh net was inserted between the two layers of coating to consolidate the unit. The total weight of an installed tracker was approximately 250 g, including the three 3.6 V primary lithium-thionyl chloride batteries (Saft, Canadian Batteries, Peterborough, ON, Canada), which corresponded to less than 2% of the body mass of the smallest beaver captured. Trackers were glued onto the lower back of the beavers using a two-component epoxy resin (Quick cure-15, System Three Resins, Lacey, WA, USA). We placed the tracker roughly 15 cm above the base of the tail, a position believed to minimize drag and increase the frequency of satellite connections with the GPS when beavers are swimming or when they emerged (Graf *et al.*, 2016). The epoxy was only applied to the guard hairs, avoiding the undercoat. This research was conducted in accordance with ASM guidelines (Sikes, 2016) and was approved by an institutional animal care and use committee.

2.2.3 Territory size

The location and size of the territory of each tracked beaver were determined by creating polygons on the basis of the readily apparent GPS data patterns using the QGIS v3.20 (QGIS Development Team 2018). A previous study suggested that standard measures of territory size, such as via Kernel methods or a minimum convex polygon, may not be appropriate for beavers because they could include unused habitats (Graf *et al.*, 2016). Although the Graf *et al.* (2016) study used the length of riverbank as a proxy for territory size, we decided it was not appropriate for our study. In Plaisance National Park, the water bodies are generally shallow bays, marshes, and ponds; therefore, an abundance of aquatic vegetation can be found across most of the territory, making it important to include water areas when estimating territory size. To confirm the GPS-derived territorial boundaries, we walked along these limits to locate the numerous scent mounts, which are used by beavers to delineate their territory (Müller-Schwarze & Heckman, 1980b). In the park, these mounds are well maintained and often very apparent at the limit of almost all territories (generally more than 10 mounts at least 30 cm high along each territorial limit). Only 1 of 25 territories lacked scent mounts. This territory was in a small pond, making it easy to confirm its boundaries. Another territory had no scent mount along two edges, but its extent could be confirmed from aerial photographs showing the canals dug by the beavers through the aquatic vegetation to reach the forest. Once the territories' boundaries were defined, polygons were created by including a 50 m land buffer around all the water portions of the territories. The only exceptions to the buffer width were produced when the buffer did not extend 50 m from the water body or when a land buffer narrower than 100 m had to be partitioned between two territories. For 3 of the 25 territories, it is possible that we had tagged a subadult because these individuals exhibited exploratory behaviors (movements far beyond the territory boundaries) several times during spring. In these three cases, the GPS positions that were clearly outside of territory boundaries on the basis of the scent mounts were removed from the data (23 points of 427 total positional data points, 43 of 643 points, and 112 of 563 points).

2.2.4 Estimation of forest and aquatic resources within territories

Forest resources — We determined the forest composition between August and September 2017. A 100 m × 100 m grid (1 ha) was overlayed on the forest map. We then sampled each grid (hectare) of forest (n = 547). In each plot, we determined the basal area of the trees having a diameter at breast height (DBH) ≥10 cm of each species using a factor 2 prism wedge at the center of the hectare. We estimated the forest resources per territory by summing all inventory plots closest to the water within each territory because beavers rarely go beyond the first 100 m from the shoreline (n = 204). However, the plots that were either shared between two territories or located along a narrow stretch of land were only counted as half hectares (therefore, the basal area was divided by two for that plot). To estimate the availability of forest resources, we divided the total basal area of each genus in each territory by the total land surface of the territory.

Aquatic resources — We estimated aquatic vegetation patch size by creating polygons with QGIS (QGIS Development Team 2018) and the cross-validation of two different sources. First, the information available on the interactive map of the wetlands of Quebec from Ducks Unlimited (Canard Illimités 2020) provided an initial estimate of the size and position of the different types of aquatic vegetation in the park. This information was updated through aerial videos produced specifically for this purpose. The video footage was obtained in August 2021 using a drone (Mavic 2 Pro, DJI) flying at 30 m altitude over the entire study area. Although the drone did not permit the creation of polygons that were as precise as the information obtained from Ducks Unlimited, the drone-derived information allowed us to update the existing maps with an inventory from the same year as the study for a month when the vegetation was most abundant. The resources available in each territory were then estimated by attributing the patches of aquatic vegetation to the territory in which they were located. Finally, we calculated the density of aquatic vegetation by dividing the surface of aquatic vegetation by the water surface in each territory and obtained the proportion of water covered by vegetation to assess aquatic resource availability.

2.2.5 Estimating beaver group size

We counted the number of beavers within each family unit using videos collected via a drone (Mavic 2 Pro, DJI) in August and September 2021. In July 2021, at least three 20-minute flights at 50 m altitude were undertaken with the drone over each family unit (either two flights in the morning and another in the evening or vice versa) so that 1) the beavers would become familiar with the sound of the drone; and 2) we could determine the best configuration for counting beavers in each territory. In August and September, two flights (one at dawn and one at dusk, each 1h20 to 1h40 in duration) were conducted over each family unit at the same altitude (50 m) as in July. When only one lodge was active for a family unit, the drone was placed in hovering flight mode so that all lodge entrances were visible. When several active lodges were situated inside a territory, the drone's camera was either orientated to cover all lodges or the drone patrolled between the lodges while keeping track of the last location known for every beaver to avoid counting individual beavers twice. For some family units located near a bridge or with several lodges, our observations involved direct observation using binoculars to complement the drone data. Through these techniques, we could reliably estimate the group size of each family unit by counting all detected individuals (kits, yearlings, subadults, and adults) (Table 2.1).

2.2.6 Statistical analysis

We produced five statistical hypotheses to test the effect of food resources on habitat quality. The first hypothesis (H1) held that aquatic vegetation is the most important food resource in a territory; therefore, the proportion of water covered by aquatic vegetation would be the best proxy for habitat quality. The next three hypotheses (H2 to H4) focus on forest food resources. H2 states that the quantity of woody resources but not its identity, *i.e.*, species, is important. Therefore, the total basal area per hectare should be the best indicator of habitat quality. The third hypothesis (H3) is similar to the second hypothesis but assumes that woody species differ in quality. In this case, habitat quality should relate to the density of ash and poplar, the genera most preferred by beavers (Rosner et al., 2022). The fourth hypothesis (H4) holds that the beavers of Plaisance National Park are specialized consumers of ash, given its high availability in the park and the strong preference of beavers for this species over other woody species (Rosner et al., 2022). In this case, only the ash basal area per hectare should reflect the habitat quality. Finally, we propose a fifth hypothesis (H5) that woody and aquatic vegetation are both important food resources for beavers. For this last hypothesis, we tested the combinations of H1 with respectively H2, H3, and H4.

To determine whether resource density affects territory size and therefore be able to discriminate between predictions 1.1 and 2.1, we produced eight linear models, relying on our five hypotheses. Territory size was tested in each of the models in regard to (H1) the proportion of aquatic vegetation (variable AV, Model 1a, Table 2.2); (H2) the total basal area per hectare (variable TBA, Model 2a, Table 2.2); (H3) the poplar basal area per hectare and the ash basal area per hectare (variables PBA and ABA, Model 3a, Table 2.2); and (H4) the ash basal area per hectare alone (Model 4a, Table 2.2). For (H5), we modelled i) the territory size with the proportion of aquatic vegetation and the total basal area per hectare (Model 5a, Table 2.2); ii) the proportion of aquatic vegetation, the poplar basal area per hectare, and the ash basal area per hectare (Model 6a, Table 2.2); and iii) the proportion of aquatic vegetation and the ash basal area per hectare (Model 7a, Table 2.2). The final model was a null model (*i.e.*, a model including only an intercept and no explanatory variable; Model 0a, Table 2.2) to verify that the selected models had a better AICc than a model without any explanatory variables.

To determine whether resource density influences group size and to discriminate between predictions 1.2 and 2.2, we re-ran the same eight models, although using group size as the predicted variable (models 0b–7b, Table 2.3). We used log-linear models with either a Poisson distribution (models 3b, 4b, and 7b) or a negative binomial distribution when the data were overdispersed (models 0b, 1b, 2b, 5b, and 6b).

For both territory and group size, we selected the models on the basis of the Akaike information criterion corrected for small sample sizes (AICc ; Burnham and Anderson 2002)). The eight models were ranked according to their AICc and their weight were calculated. We then realized a multimodel inference to determine the variables that had an effect on group and territory size by a method of full model averaging, which allows to mitigate the incertainty of the models and provide a more robust assessment of the effect of each predictor (Burnham and Anderson 2002). All the models were realized on R software (R Development Core Team 2020).

2.3 Results

2.3.1 Territory and group size determination

The average territory size was 17.4 ± 9.1 ha (range 2.4 – 39.1 ha). Only four territories were smaller than 10 ha, and three larger than 30 ha (Table 2.1). Overall, the territories showed almost no overlap between colonies (Figure 2.3). The average group size was 8.1 ± 3.8 beavers per group (range 3 – 17) (Table 2.1). There was no significant relation between the territory size and the group size when tested with a Pearson's correlation ($r = 0.34$, $p = 0.10$).

Table 2.1 : Overview of the 25 beavers captured and equipped with a GPS tag in the spring of 2021 in Plaisance National Park, Quebec, Canada; data includes the associated territory and group size

Sex	Weight (kg)	Number of tracking nights	Number of GPS positions	Territory size (ha)	Group size
Female	20.0	13	195	16.8	8
Male	21.0	20	684	8.2	8
Male	21.4	12	214	10.2	6
Male	15.2	17	441	14.8	14
Male	20.5	9	111	10.3	11
Female	20.5	19	553	5.6	5
Male	20.0	21	493	13.5	12
Female	17.0	25	643	10.7	7
Male	18.4	25	451	19.0	4
Male	18.5	36	990	32.3	9
Female	19.7	29	600	39.1	11
Male	20.0	11	333	15.3	13
Female	21.0	8	185	10.8	6
Male	21.0	32	728	27.1	5
Male	19.0	18	435	21.9	17
Male	22.0	12	319	10.5	4
Male	20.0	19	394	18.3	8
Female	21.5	15	368	24.0	14
Female	21.8	15	302	32.4	11
Male	25.0	21	404	15.0	7
Male	21.4	8	214	20.1	5
Male	23.5	5	76	2.4	3
Female	25.0	20	224	21.7	5
Male	22.0	9	159	8.7	3
Female	22.0	12	339	27.0	6

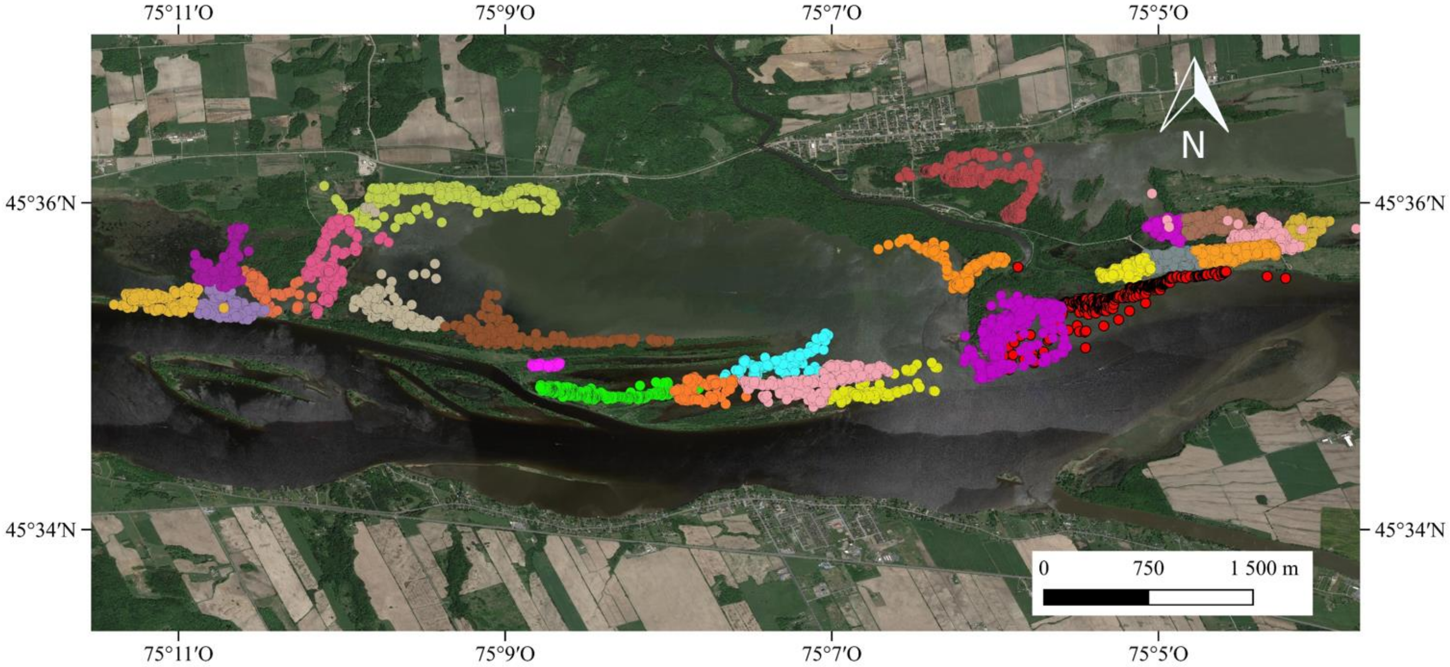

Figure 2.3 Map showing the GPS positions of the 25 beavers equipped with a GPS tag in Plaisance National Park, Quebec, Canada, between April and July 2021. The few points far outside a territory have been deleted for three beavers. Each color represents a different individual.

2.3.2 Territory size

The averaged model had an intercept of 21.74 (*CI*: 10.49 – 33.00) but no predictors had an effect on the territory size as all their *CI* included 0 (Table 2.3), which did not support the negative relation between territory size and resource density (Prediction 1.1).

Table 2.2 Comparison of models predicting the territory size of beaver colonies in Plaisance National Park, Quebec. The explanatory variables are the proportion of aquatic vegetation per ha of water (AV), the total basal area per ha (TBA), the basal area of poplar per ha (PBA), and the ash basal area per ha (ABA). The Akaike's information criterion corrected for small sample sizes (AICc), the ΔAICc, and the weight of each model are indicated. The two best models are in bold.

Model	Formula	Number of parameters (K)	AICc	ΔAICc	Weight
1a	$\boldsymbol{Y=\beta_0+\beta_1AV}$	**3**	**183.99**	**0.00**	**0.37**
0a	$\boldsymbol{Y=\beta_0}$	**2**	**184.95**	**0.96**	**0.23**
5a	$Y=\beta_0+\beta_1AV+\beta_2TBA$	4	186.27	2.28	0.12
7a	$Y=\beta_0+\beta_1AV+\beta_4ABA$	4	186.33	2.34	0.11
2a	$Y=\beta_0+\beta_2TBA$	3	187.16	3.17	0.07
4a	$Y=\beta_0+\beta_4ABA$	3	187.50	3.51	0.06
6a	$Y=\beta_0+\beta_1AV+\beta_3PBA+\beta_4ABA$	5	189.49	5.50	0.02
3a	$Y=\beta_0+\beta_3PBA+\beta_4ABA$	4	190.25	6.27	0.02

Table 2.3 : Model-averaged predictors based on the 8 tested models to explain the territory size (Table 2.2) with the estimates, the standard errors and the 95% confidence interval for the proportion of aquatic vegetation per ha of water (AV), the total basal area per ha (TBA), the basal area of poplar per ha (PBA), and the ash basal area per ha (ABA).

Variables	Estimate	Standard error	95% Confidence interval
Intercept	**21.74**	**5.74**	**(10.49 - 33.00)**
AV	-7.60	7.85	(-22.98 - 7.78)
TBA	0.02	0.06	(-0.11 - 0.14)
ABA	0.03	0.15	(-0.27 - 0.33)
PBA	0.01	0.20	(-0.38 - 0.39)

2.3.3 Group size

The averaged model had an intercept of 1.73 (*CI*: 1.41 – 2.05) with an effect of ash density (m^2/ha) of 0.03 (*CI*: 0.01 – 0.06). Hence, ash basal area per hectare (ABA), had a positive effect on group size (Figure 2.5), as its *CI* did not include zero (Table 2.4). Model 4b

Table 2.4 Comparison of models predicting group size of beaver colonies in Plaisance National Park, Quebec. The explanatory variables are the proportion of aquatic vegetation per ha of water (AV), the total basal area per ha (TBA), the basal area of poplar per ha (PBA), and the ash basal area per ha (ABA). The Akaike's information criterion corrected for small sample sizes (AICc), the ΔAICc, and the weight of each model are indicated. The best model is in bold.

Model	Formula	Number of parameters (K)	AICc	ΔAICc	Weight
4b	**$Y=\beta_0+\beta_4 ABA$**	**2**	**131.84**	**0.00**	**0.60**
3b	$Y=\beta_0+\beta_3 PBA+\beta_4 ABA$	3	134.41	2.57	0.16
7b	$Y=\beta_0+\beta_1 AV+\beta_4 ABA$	3	134.43	2.59	0.16
2b	$Y=\beta_0+\beta_2 TBA$	3	137.98	6.14	0.03
0b	$Y=\beta_0$	2	138.70	6.86	0.02
6b	$Y=\beta_0+\beta_1 AV+\beta_3 PBA+\beta_4 ABA$	5	139.54	7.70	0.01
5b	$Y=\beta_0+\beta_1 AV+\beta_2 TBA$	4	140.35	8.51	0.01
1b	$Y=\beta_0+\beta_1 AV$	3	140.71	8.87	0.01

Table 2.5 : Model-averaged predictors based on the 8 tested models to explain the group size (Table 2.2) with the estimates, the standard errors and the 95% confidence interval for the proportion of aquatic vegetation per ha of water (AV), the total basal area per ha (TBA), the basal area of poplar per ha (PBA), and the ash basal area per ha (ABA).

Variables	Estimate	Standard error	95% Confidence interval
Intercept	**1.73**	**0.16**	**(1.41 - 2.05)**
ABA	**0.03**	**0.01**	**(0.01 - 0.06)**
PBA	< 0.01	0.01	(-0.03 - 0.03)
AV	0.01	0.13	(-0.25 - 0.27)
TBA	< 0.01	< 0.01	(-0.01 - 0.01)

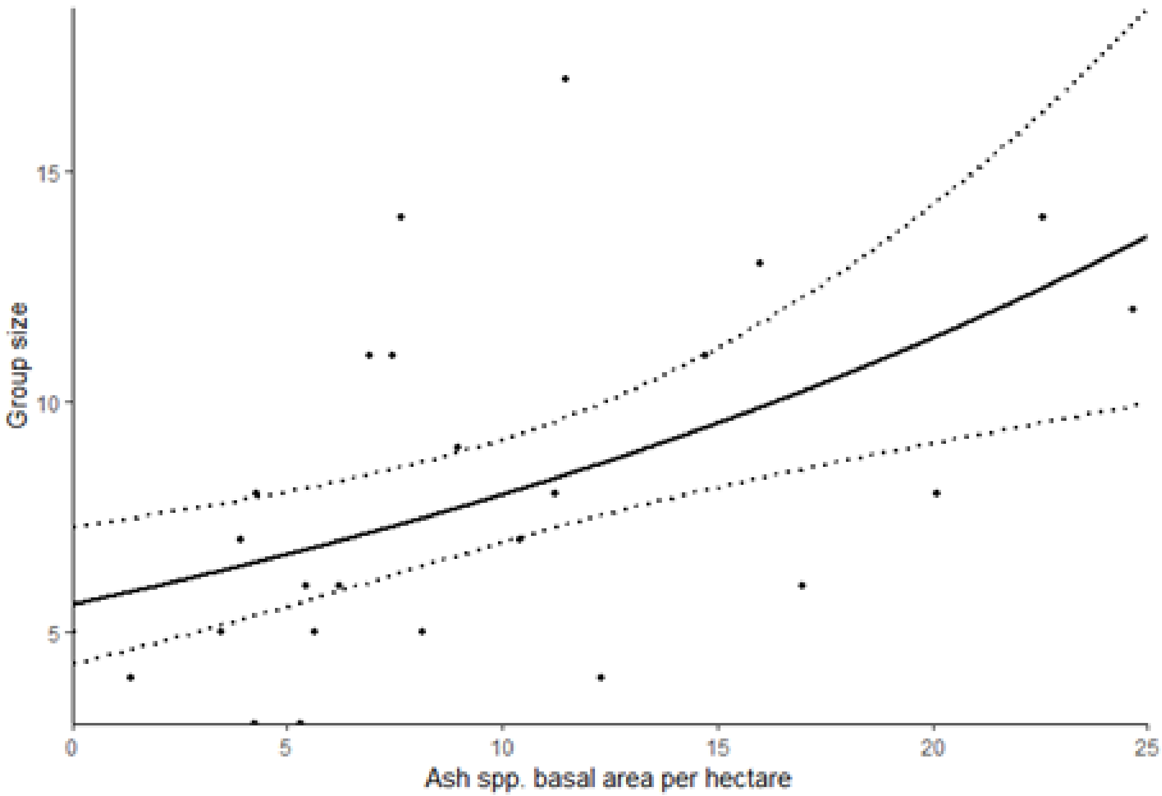

Figure 2.4 Effect of ash basal area (m2/ha) on group size for 25 beaver colonies in Plaisance National Park, Quebec, counted in 2021 (solid line), with the 95% confidence intervals (dotted lines) calculated from the equation of averaged model, the relationship is strictly positive as ash density CI values (0.01-0.06) did not intercept 0. (Table 2.5).

2.4 Discussion

In this study, our central question was whether food resources influence Canadian beaver territory size, group size, or both. This question is of general relevance because there is no consensus to explain the underlying mechanisms involved in the relationship between habitat quality and the density and spatial distribution of territorial social species (Kittle *et al.*, 2015; Kruuk & Parish, 1982). Our results indicate that resource density of either aquatic vegetation or trees (namely ash species), had no significant effect on beaver territory size (Prediction 2.1). However, a positive effect on group size of beaver colonies (Prediction 2.2) was found for the Plaisance National Park. Together, these two results suggest that mechanism 2 characterized by increase of family group size with increases in resource abundance with no effect on territory size (Fig. 1) is likely the one at play for explaining patterns of population density measured in riparian ecosystems of our study area. Our results are thus link with the resource dispersion hypothesis.

Few studies have demonstrated that resources availability regulate the densities of territorial species through group size and not territory size. Our finding is consistent with previous studies showing that fitness or group size increases with increasing resource availability (Fryxell, 2001; Smith, 1997). However, these studies did not simultaneously test for the effect of resource availability on territory size and thus, cannot be used to discriminate between mechanisms 2 and 3 (Figure 2.1). Other studies have shown that more resources increased colony density, *i.e.*, the number of independent family units in a given area, which implies that territory size decreased. However, these studies did not estimate the number of beavers in each colony, *i.e.*, the group size (Smith and Tyers 2012, Bergman *et al.* 2018). Moreover, colony densities in these two studies was estimated by counting active lodges. However, beaver colonies can have several active lodges (Müller-Schwarze, 2011) that can also be quite distant from one another. For instance, in our study, active lodges belonging to the same colony were sometimes located more than 350 m apart. Thus, the number of lodges in these earlier studies could reflect family group size instead of territory size. Kruuk and Parish (1982) observed that badgers (*Meles meles*) respond to increased resource availability by increasing their group size, a prediction made by the resource dispersion hypothesis. However, more recent studies with the same species disproved that badgers respond according to this hypothesis (Revilla & Palomares, 2002; Robertson *et al.*, 2015). This discrepancy between studies may imply that a territorial species can regulate its density through group or territory size depending on yet unknown conditions. Therefore, this could be another explanation for the discrepancy between our results and other studies that found resource availability drives colony density (Bergman *et al.*, 2018; Smith & Tyers, 2012). Eventhough the absence of relationship between resource availability and territory size may appear surprising, this result is somewhat consistent with Campbell *et al.* (2005) where similar results were observed for Eurasian beavers (*i.e.*, habitat quality did not influence negatively territory size). However, in Campbell *et al.* (2005) study, Eurasian beavers showed a positive relation between habitat quality and territory size, and a negative correlation between the settlement date and the territory size, suggesting that the first colonies to settle could secure larger territories of higher quality.

Our findings do not support several hypotheses of territoriality. Given the investment that beavers make to mark and defend their territory (Herr & Rosell, 2004; Nolet & Rosell, 1994; Rosell & Thomsen, 2006) and our observations that beavers in Plaisance National Park make very few incursions into adjacent territories, we would expect that greater resource availability be inversely related to territory size, as predicted by the economic defendability hypothesis (Brown, 1964).

Studies of territorial social species have shown that resource availability can affect territory size without influencing group size (Kittle *et al.*, 2015; Patterson & Messier, 2001). One explanation put forward by Kittle *et al.* (2015) is that the costs of territoriality may outweigh the benefits of a larger group size. It is possible, therefore, that in the case of beavers—and potentially other territorial social species—the opposite is applicable, *i.e.*, that the benefits of securing large amounts of resources and increasing group size outweigh the costs of maintaining territory size. Several reasons could be advanced to explain this phenomenon. For example, increasing group size may diminish the cost of territoriality, either because juveniles are actively involved in patrolling and defense—although that help is minimal (Hohwieler *et al.*, 2018)—or simply because participation in alloparental care by the juveniles and subadults (Müller-Schwarze, 2011) could provide more time for breeding individuals to defend the territory. It is also possible that certain phenomena reduce the daily costs of territoriality, such as the "dear enemy" effect, which has been observed in beavers (Rosell & Bjørkøyli, 2002) and which reduces the intensity of aggressive responses when the intruder is a known neighbor (Tumulty, 2018). The diminution of the aggressive responses could result in a diminution of the territoriality cost, allowing beavers to defend a large territory. Finally, when a territory is available, beavers may tend to settle close to their parental colony (Sun *et al.* 2000). Thus, kinship may play a role in reducing the cost of territoriality. Beavers can recognize their relatives by their sense of smell, and aggressive reactions to their scent are reduced compared with reactions to an unrelated individual's scent (Sun and Müller-Schwarze 1997). Although the underlying process has not yet been identified, it seems that the costs of territoriality may be reduced for some territorial social species, but further studies are needed to understand the underlying mechanisms of this pattern.

Put in the context of invasion by emerald ash borer, our results suggest a likely decrease in group size because of the positive effect of ash tree density on group size. It is therefore predicted that the density of beaver populations will decrease with a decline in ash species. However, this decrease is unlikely to be spatially constant and will depend highly on local conditions of ash trees as a forage resource. Ash trees can be very abundant in temperate riparian forests but their distribution may vary spatially. Indeed, in our study site, except for a single beaver territory having no ash trees, the basal area of ash varied between 13% and 84% among territories. Thus, our conclusions regarding ash trees being the sole important resource apply only to temperate riparian forests largely dominated by ash. It is likely that the loss of ash in forests where it represents only a small proportion of the trees will not be important for beaver populations. In ash-dominated riparian forests, the potential effect of ash loss on beaver populations will also depend on the tree species that replace ash. For example, if the ash trees are replaced by poplars and willows, which are pioneer species, there may be little or no impact on beaver populations, given the beaver's preference for these species (Hall, 1960; Vorel *et al.*, 2015). On the other hand, if ash is replaced by species such as silver maple (*Acer saccharinum*), which is one of the most abundant species in our study site, beaver populations would likely decrease, as beavers do not consume this species in such habitats (Barnes & Dibble, 1988; Rosner *et al.*, 2022). If the latter occurs, our findings suggest that in ash-dominated temperate riparian forests, the loss of ash may reduce the number of individuals per family unit; however, the total number of groups may remain stable.

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2.6 References

Aleksiuk, M., and I. M. Cowan. 1969. Aspects of seasonal energy expenditure in the beaver (Castor canadensis Kuhl) at the northern limit of its distribution. Canadian Journal of Zoology 47:471–481.

Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany 66:40–44.

Bergman, B. G., J. K. Bump, and M. C. Romanski. 2018. Revisiting the role of aquatic plants in beaver habitat selection. American Midland Naturalist 179:222–246.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. The Wilson Bulletin:160–169.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. . Springer-Verlag. New-York.

Calsbeek, R., and B. Sinervo. 2002. An experimental test of the ideal despotic distribution. Journal of Animal Ecology 71:513–523.

Canards Illimités Canada et le ministère de l'Environnement et Lutte contre les changements climatiques (MELCC), 2020. Cartographie détaillée des milieux humides des secteurs habités du sud du Québec – Données du projet global [ESRI Canada], Québec (Québec).

Cury, P. M. *et al.* 2011. Global seabird response to forage fish depletion - One-third for the birds. Science 334:1703–1706.

DeStefano, S., K. K. G. Koenen, C. M. Henner, and J. Strules. 2006. Transition to independence by subadult beavers (Castor canadensis) in an unexploited, exponentially growing population. Journal of Zoology 269:434–441.

Engelken, P. J., and D. G. McCullough. 2020. Riparian forest conditions along three northern Michigan rivers following emerald ash borer invasion. Canadian Journal of Forest Research 50:800–810.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–35.

Fryxell, J. M. 2001. Habitat suitability and source–sink dynamics of beavers. Journal of Animal Ecology 70:310–316.

Graf, P. M., M. Mayer, A. Zedrosser, K. Hackländer, and F. Rosell. 2016. Territory size and age explain movement patterns in the Eurasian beaver. Mammalian Biology 81:587–594.

Hall, J. G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology 41:484–494.

Herr, J., and F. Rosell. 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (Castor fiber). Journal of Zoology 262:257–264.

Herrera, E. A., V. Salas, E. R. Congdon, M. J. Corriale, and Z. Tang-Martínez. 2011. Capybara social structure and dispersal patterns: Variations on a theme. Journal of Mammalogy 92:12–20.

Hohwieler, K., F. Rosell, and M. Mayer. 2018. Scent-marking behavior by subordinate Eurasian beavers. Ethology 124:591–599.

Huxley, J. S. 1934. A natural experiment on the territorial instinct. British Birds 27:270–277.

Johnson, C. J. 2013. Identifying ecological thresholds for regulating human activity: Effective conservation or wishful thinking? Biological Conservation 168:57–65.

Johnson, D., R. Kays, Blackwell, Paul G, and D. W. Macdonald. 2002. Does the resource dispersion hypothesis explain group living? Trends in Ecology and Evolution 17:563–570.

Johnson, M. D. 2007. Measuring Habitat Quality: A Review. The Condor 109:489–504.

Johnston, C. A., and R. J. Naiman. 1990. Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research 20:1036–1043.

Kittle, A. M. *et al.* 2015. Wolves adapt territory size, not pack size to local habitat quality. Journal of Animal Ecology 84:1177–1186.

Kruuk, H., and T. Parish. 1982. Factors affecting population density-, group size and territory size of the European badger, Meles meles. Journal of Zoology 196:31–39.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379–384.

Mayer, M., C. Aparicio Estalella, S. K. Windels, and F. N. Rosell. 2020a. Landscape structure and population density affect intraspecific aggression in beavers. Ecology and Evolution 10:13883–13894.

Mayer, M., S. C. Frank, A. Zedrosser, and F. Rosell. 2020b. Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. Journal of Animal Ecology 89:577–588.

Milligan, H. E., and M. M. Humphries. 2010. The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. Oikos 119:1877–1886.

Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer. 2009. Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. Ecology Letters 12:1050–1060.

Müller-Schwarze, D., and S. Heckman. 1980. The social role of scent marking in beaver (Castor canadensis). Journal of Chemical Ecology 6:81–95.

Müller-Schwarze, D. 2011. The Beaver: Natural history of a wetlands engineer. 2nd edition. Comstock Publishing Associates.

Nolet, B. A., and F. Rosell. 1994. Territoriality and time budgets in beavers during sequential settlement. Canadian Journal of Zoology 72:1227–1237.

Patterson, B. R., and F. O. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. Journal of Mammalogy 82:463–477.

Payne, N. F. 1982. Colony size, age, and sex structure of Newfoundland beaver. The Journal of Wildlife Management 46:655–661.

QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. https://www. qgis.org/en/site/.

R Development Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/.

Revilla, E., and F. Palomares. 2002. Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, Meles meles. Journal of Animal Ecology 71:497–512.

Robertson, A., K. L. Palphramand, S. P. Carter, and R. J. Delahay. 2015. Group size correlates with territory size in European badgers: Implications for the resource dispersion hypothesis? Oikos 124:507–514.

Rosell, F., and T. Bjørkøyli. 2002. A test of the dear enemy phenomenon in the Eurasian beaver. Animal Behaviour 63:1073–1078.

Rosell, F., and L. R. Thomsen. 2006. Sexual dimorphism in territorial scent marking by adult Eurasian beavers (Castor fiber). Journal of Chemical Ecology 32:1301–1315.

Rosner, S., A. Dupuch, and F. Lorenzetti. 2022. Stuck between the mandibles of an insect and of a rodent: where does the fate of ash-dominated riparian temperate forests lie? Forests 13:1760.

Sikes, R. S. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Allen Press Inc. Journal of Mammalogy.

Smith, D. W. 1997. Dispersal strategies and cooperative breeding in beavers. University of Nevada, Reno.

Smith, D. W., and D. B. Tyers. 2012. The history and current status and distribution of beavers in Yellowstone National Park. Northwest Science 86:276–288.

Sun, L., D. Müller-Schwarze, and B. A. Schulte. 2000. Dispersal pattern and effective population size of the beaver. Canadian Journal of Zoology 78:393–398.

Tumulty, J. P. 2018. Dear enemy effect. Pp. 1–4 in Encyclopedia of animal cognition and behavior. Springer International Publishing.

Vorel, A., L. Válková, L. Hamšíková, J. Maloň, and J. Korbelová. 2015. Beaver foraging behaviour: Seasonal foraging specialization by a choosy generalist herbivore. Behavioral Ecology and Sociobiology 69:1221–1235.

CHAPITRE 3

COMMUNITIES OF LITTER INVERTEBRATES WILL BE AFFECTED BY THE DISAPPEARANCE OF ASH TREES IN TEMPERATE RIPARIAN FORESTS

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RÉSUMÉ

L’invasion de l’Amérique du Nord par l’agrile du frêne (*Agrilus planipennis*) va causer la disparition de la quasi-totalité des frênes (*Fraxinus* spp.). Ce genre peut être très abondant, voire dominant, dans les forêts ripariennes du sud du Québec qui possèdent une litière de qualité. En effet, leur litière est généralement reconnue comme ayant une vitesse de décomposition très élevée, ce qui peut favoriser certaines espèces d’invertébrés. La plupart des études portant sur les effets de la disparition du frêne sur les invertébrés s’intéressent généralement à des taxons en particulier, et étudient davantage les effets de la modification structurelle de la forêt (ouverture de la canopée, augmentation de la quantité de bois mort) que les effets de la modification de la litière. Dans la présente étude, nous avons cherché à déterminer si le frêne est bien le genre qui détermine la vitesse de décomposition dans une litière composée majoritairement de frênes et d’érables (*Acer* spp.), mais également si au-delà de la structure de la forêt, la modification de la litière pourrait également avoir des effets sur les communautés d’invertébrés, que ce soit sur la diversité des familles présentes, sur la composition des assemblages, ou sur leur richesse taxinomique. Nous avons sélectionné huit sites au parc national de Plaisance (Québec, Canada) qui représentaient un gradient de densité de frênes, et dans lesquels nous avons échantillonné des parcelles qui étaient coupées pour simuler l’effet de la mort des arbres, des parcelles qui étaient adjacentes aux parcelles coupées, et des parcelles témoins. Les invertébrés ont été piégés dans des pièges-fosses et identifiés par une méthode de métabarcoding, ce qui a permis d'étudier la plupart des taxons présents. Nous avons pu mettre en évidence que le frêne était bien le genre taxinomique qui est déterminant dans la vitesse de décomposition de la litière, et que le frêne avait bel et bien une importance pour les communautés d’invertébrés de cette litière. En moyenne, les parcelles dans lesquelles les frênes étaient abondants avaient une diversité de familles d’invertébrés légèrement moins importante, mais les assemblages de familles étaient également différents, montrant que certaines communautés associées aux frênes sont singulières à ce genre. Enfin, certaines familles avaient une diversité taxinomique influencée positivement pas la vitesse de décomposition de la litière, ce qui implique que la disparition des frênes pourrait avoir des effets négatifs sur la biodiversité à l’échelle des forêts de la zone riparienne.

Mots-clés: Agrile du Frêne, Invertébrés de la litière, Vitesse de décomposition de la litière, Forêt riparienne, Frêne, Perturbation

ABSTRACT

The invasion of emerald ash borer (*Agrilus planipennis*) in North America will likely cause the disappearance of almost all ash trees (*Fraxinus* spp.). This genus can be very abundant, even dominant, in riparian forests of southern Quebec, and has a high-quality litter. Indeed, its litter is generally recognized as having a very high decomposition rate, which can favor certain invertebrate species. Most studies on the effects of ash disappearance on invertebrates focused on specific taxa, and were more concerned of the effects of structural changes in the forest (canopy opening, increase in dead wood, increase in herbaceous cover) than the effects of changes in litter properties. In the present study, we sought to determine whether ash is indeed the genus that determines the decomposition rate in a litter composed predominantly of ash and maple (*Acer* spp.). We were also interested to examine if litter modification could impact invertebrate communities, whether on the richness of invertebrate families present, on the composition of assemblages, or on their taxonomic richness. We selected eight sites in Parc national de Plaisance (Quebec, Canada) that represented an ash tree basal area gradient, and in which we sampled plots that were cut to simulate the death of trees, plots that were adjacent to the cut plots, and control plots. Invertebrates were captured with pitfall traps and identified through a metabarcoding method, allowing us to study most of the taxa that were present. We found that ash was indeed the genus that determined the rate of litter decomposition and that was important for invertebrate communities. On average, plots in which ash was abundant had slightly lower family richness, but family composition of assemblages were also different, showing that ash-associated communities are singular. Finally, some families had a taxonomic diversity positively influenced by litter decomposition rate, implying that the disappearance of ash could have negative effects on biodiversity at the riparian forest scale.

Key words: Emerald ash borer, soil invertebrates, litter decomposition rate, riparian forest, ash tree, disturbance

3.1 Introduction

Riparian forests are ecotones at the interface between terrestrial and aquatic environments. They are considered critical transition zones because despite their small size, their function such as sediment retention or nutrient supply (Gregory et al., 1991; Naiman & Decamps, 1997), expands beyond their physical limits(Hunter *et al.*, 2017). Furthermore, riparian forests are known to harbour a high biodiversity of both animal and plant species (Forio *et al.*, 2020; Maisonneuve & Rioux, 2001; Paine & Ribic, 2002). In North America, particularly in eastern temperate forests, many riparian forests are dominated by ash species (*Fraxinus* sp.) and will therefore be greatly impacted by the emerald ash borer (EAB, *Agrilus planipennis*, Fairmaire; Engelken & McCullough, 2020).

The EAB is an invasive exotic insect that was introduced to North America in the 1990s (Siegert *et al.*, 2014). All species of ash trees in North America are susceptible to this insect, which will lay its eggs under the bark of these trees, and whose larvae will feed on the phloem. The consequences are that the infested trees will die in the years following the initial attack. The spread of the damage by this insect is very rapid as the mortality of virtually all ash trees in a stand can occur within six years of the initial infestation (Knight *et al.*, 2013).

The impact of EAB on ash-dominated riparian forests is likely to be significant for several reasons. From a physical standpoint, the loss of ash will have short- to medium-term changes, such as a sudden opening of the canopy, an increase in the amount of dead wood (Perry, Herms, *et al.*, 2018), and most likely an increase in the herbaceous cover stimulated by the canopy gaps (Kelemen *et al.*, 2012). Those effects can be considered short- to medium-term changes because after some years, other trees should fill the canopy gaps, which will decrease the amount of herbaceous cover. Even woody debris will also eventually decompose, even if this takes several decades, ash trees being known to have a relatively fast decay rate (Aulen *et al.*, 2012; Harmon & Sexton, 1996; Lasota *et al.*, 2022; Perry, Herms *et al.*, 2018). Other effects will be long term or even potentially permanent changes, such as the composition of the forest. Therefore, the litter composition will also be altered and will likely have different properties than the former one. Ash trees are known to have relatively labile litter, *i.e.*, a high decomposition rate, compared to other species. For example, black ash (*Fraxinus nigra* Marshall) has a more labile litter than silver maple (*Acer saccharum* Marsh) or aspen (*Populus tremuloides* Michx), which can be beneficial for some invertebrates (Palik *et al.*, 2005). However, the litter decomposition rate within the same genus may depend on the age, the species of the trees, and even the location of the trees within the same species (Jonczak, 2009; Lecerf & Chauvet, 2008; Leroy et al., 2007).

These EAB-induced habitat changes have the potential to impact animal communities, such as birds and mammals (e.g., Grinde *et al.*, 2022). Litter invertebrate communities could also be altered given that they are influenced by canopy openness (Černecká *et al.*, 2020; Perry, Wallin, *et al.*, 2018), amount of coarse woody debris (Grodsky *et al.*, 2018b), and litter composition (Koivula *et al.*, 1999; Laird-Hopkins *et al.*, 2017; Sayer *et al.*, 2010; Vauramo & Setälä, 2011). A previous study has already shown that 43 species of arthropods are entirely dependent on the presence of ash trees, and that more than 200 other species are likely to be impacted by its disappearance (Gandhi & Herms, 2010b). Although we know that dozens of invertebrate species depend on ash in their habitat, we do not understand how the disappearance of ash trees in riparian forests will influence invertebrate communities. Answering this question is essential given that invertebrates play crucial roles in forests, through decomposition of the litter (Hättenschwiler *et al.*, 2005b) and coarse woody debris (Ulyshen, 2016), and even soil structuring (Jouquet *et al.*, 2006). In riparian forests, these roles may be even more important because invertebrates are consumed in both terrestrial and aquatic foodwebs (Collier *et al.*, 2002; Murakami & Nakano, 2001; Ramey & Richardson, 2017; Wipfli, 1997).

Estimating invertebrate biodiversity can be long and difficult, as many species are hard to distinguish from each other morphologically (Gerlach *et al.*, 2013). Therefore, this task can require the help of several taxonomists to assess the biodiversity of a large spectre of taxa. In the last few years, studies based on DNA metabarcoding have been increasingly used because they allow one to have a comprehensive assessment of the community in a short time frame (Ji *et al.*, 2013). The study of species diversity can be very complex, even at the genetic level, because the limits of what is a species are sometimes blurred, and because there is not a single definition for what a species is (Blaxter, 2004). For these reasons, more and more studies are focusing on the taxonomic diversity of taxa, often estimated using unique nucleotide sequences: Amplicon Sequence Variants (hereafter ASVs) (eg O’Brien *et al.*, 2020; Steyaert *et al.*, 2020).

The objectives of this study will be to determine: (1) if litter composed of ash leaves has a higher decomposition rate than litter composed of maple leaves. If so, we should observe that litters with a higher ash content decay faster than those with a high content of maple leaves; (2) if the effects induced by the extinction of ash trees (both on the forest structure and on the properties of the litter) influence the diversity and composition of ground-dwelling invertebrates communities present in riparian forests.

3.2 Materials and Methods

3.2.1 Study site

The study was conducted in Plaisance National Park, Quebec, Canada, an area of 28 km^2 located along the Ottawa River (Figure 3.1). The park is composed of several low-lying peninsulas and small islands, so much of the 400 ha of forest is riparian. A detailed inventory of the park revealed that about half of the forest's basal area is composed equally of ash (*Fraxinus* spp.) and maple (*Acer* spp.), while the other half is composed of more than 43 tree species, making it a very diverse forest (*F. Lorenzetti, unpublished results*). A more precise description of the study site, especially the forest composition can be found in chapter 1 and in Rosner *et al.* (2022).

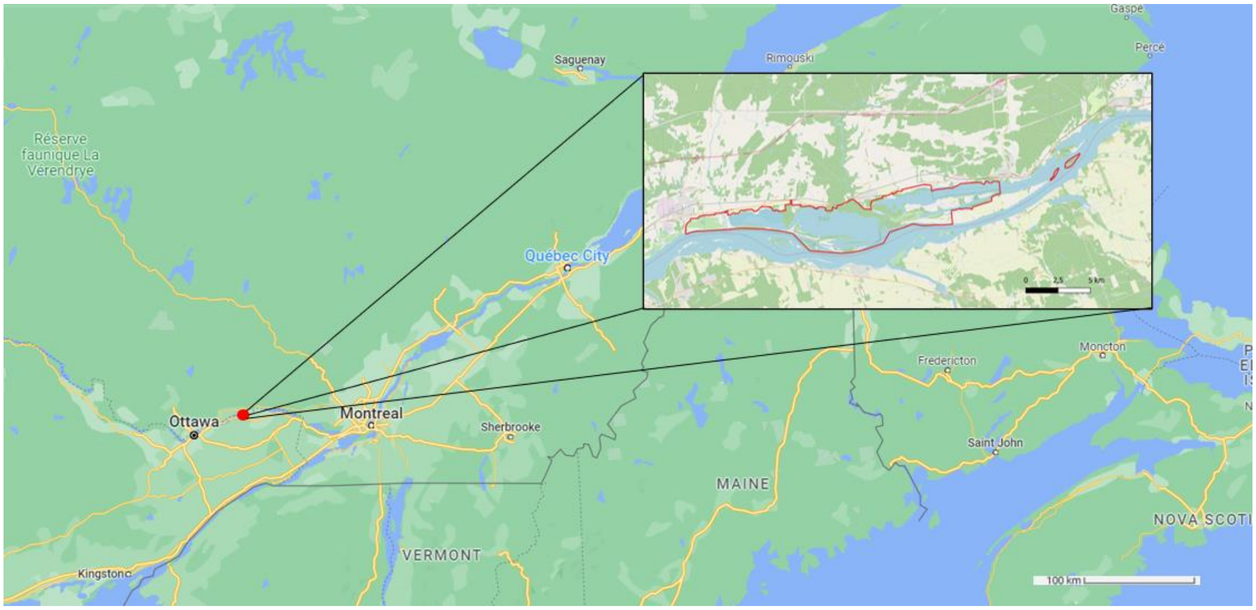

Figure 3.1 Location of Plaisance National Park on the Ottawa River, Quebec, Canada. Insert: park limits are drawn with a red line. Maps are based on images from Google, 2022 (large scale) and OpenStreetmap (small scale).

3.2.2 Experimental design

Eight plots of 0.4-0.8 ha (median surface area of 539 m^2) minimally spaced 70 m between each plot were selected across the park to represent opposing gradients of basal area of ash (mainly *Fraxinus americana* L.) and maple (mainly *Acer saccharinum* L.) trees (diameter at breast height thereafter called DBH>10 cm). The proportion of ash basal area varied from 12 to 100% and that of maple from 0 to 88%. The median basal area proportion of other species when present was 16.8% (range = 1.4 to 22.4%). In the fall of 2017, all trees were cut to simulate the effect of the perturation, and the biomass was left on the site. Each cut plot represented the center of a sampling area where around each cut plot, four additional adjacent plots of equal area were delimited (one at each of the cardinal directions), and a fifth 50 m away from the cut plot to serve as a control. The control plot was set at the same distance from the water as the cut plot, and in stand with a similar forest composition. The fact that all the trees were cut and not just the ash trees in the cut plot allows to differentiate between the effect of the disappearance of ash litter and the effect of the canopy gap creation. In total, there were eight sampling areas composed of 6 plots, for a total of 48 plots. Of the 48 plots, one was in a field and therefore not considered in the study since not representative of a forest habitat. Overall, this design allowed the discrimination between the effect caused by the death of the trees (our eight cut plots) and the effect of the litter modification between sites with no ash trees and those with different basal area of live ash trees.

3.2.3 Habitat attributes

During the summer of 2019, all stems of tree species (DBH>1cm) had their DBH measured to the nearest centimeter and were identified to species on each of the 48 plots. Canopy openness was measured from digital hemispherical images when the foliage of the different species was fully developed. The camera was placed at 1m above ground in the center of each plot. Photographs (f 2.8, ISO 200) were analyzed with ImageJ software to determine the precise canopy openness (Xiong *et al.*, 2019). The average herbaceous cover was estimated inside a five-meter diameter circle around each pitfall trap placed to collect ground dwelling invertebrates. Classes of cover were attributed to each pitfall trap (0%; less than 5%; 5 to 25% ; 25 to 50%, 50 to 75%, and more than 75%). Midclass values were then assigned and averaged over the four pitfall traps placed in a plot, yielding an estimate of the percentage of cover for each plot. The quantity of coarse woody debris was estimated inside the same circle, by realizing two perpendicular transects and measuring the diameter of every coarse woody debris (≥9 cm). The estimation was realized with the equation of de Vries (1973).

3.2.4 Estimation of litter decomposition rate

In each of the eight cut plots, three litter traps were installed (75x75 cm) in the fall of 2018 to determine the proportion of litter from ash, maple, and other tree genera. All leaves collected from each litter trap were dried in an oven at 40ºC for 72 hours, identified to species, and weighed. Genera other than ash and maple spp. were never dominant in the litter and represented between 9 and 48% of the dried collected biomass depending on the site (median value of 16.7%). Because it was difficult to replicate litter including samples of each of the genera in the right proportion, it was decided to consider only the proportion of ash and maple spp. found in the litter traps. This means that a site that had its litter split 40% ash, 40% maple and 20% other species would be considered 50% ash and 50% maple.

In order to estimate litter decomposition rate, ash spp. and maple spp. leaves were collected in September 2019 from each of the eight sites and dried using the same method as the previous year.

In each cut plot were placed 30 litter bags made of 1mm-mesh solid plastic and containing 3g of litter in the relative proportion that was determined. The litter bags were placed on the ground in the middle of each cut plot and five of them were collected in November 2019, and then after the winter, five bags were collected in each of the months of May, June, August, September, and October of 2020. Once collected, the bags of litter were dried using the same method and the content weighed.

3.2.5 Invertebrates sampling and DNA extraction

In each of the 47 plots, four pitfall traps were installed at least 6m apart, and 6m from the edge of the plot. The traps were filled with 100ml of propylene glycol (Dow PuraGuard™ Propylene glycol USP/EP, Agro-bio Contrôle, St-Hyacinthe, Qc, Canada). Pitfall traps were set in early July 2019, and were harvested every two weeks until the end of September, and the contents were stored in a cold room (5 ºC) until processing.

After the last harvest, all samples from each single trap were pooled and transferred to a Buchner funnel connected to a vacuum pump, so that all propylene glycol could be extracted from the mass of invertebrates. The Buchner funnel was fitted with a filter (Pall Laboratory, 47mm A/D glass filter, 3.1um; VWR Canada). To extract as much of the remaining propylene glycol from the sample as possible, enough 70% ethanol was first added to the Buchner funnel to submerge the sample, and after standing for 10 minutes, the ethanol was filtered out with the vacuum pump. The same process was performed with 100% ethanol to pursue the extraction. After this last filtration, the sample was placed on a Whatman #4 filter paper (VWR Canada) until all the remaining ethanol was evaporated. The invertebrate sample was then mixed with a buffer solution (0.4M NaCl, 10mM tris-HCl, 2mM EDTA, pH8) at a 1:1 ratio with the volume of invertebrates, and ground with a homogenizer (Fisherbrand™ 850, Fischer Scientific Canada) equipped with a wide window stainless-steel probe (Fisherbrand™ Saw Tooth 20 x 115 mm (Coarse) Generator Probe, Fischer Scientific Canada). Grinding was performed for 30 seconds at 7000 rpm, followed by 10 seconds at 9000 rpm. Between each sample, the probe was cleaned with a 1% sodium hypochlorite solution, rinsed with distilled water, and sterilized with a blowtorch. Samples were then stored at -70ºC until DNA extraction. DNA was extracted using the salt extraction method described by Aljanabi & Martinez (1997). Following the extraction, a 440bp fragment of the Cytochrome Oxydase I gene

(COI) was amplified as described in Beng *et al.* (2016) and sent to the Centre d'expertise et de services de Génome Québec for sequencing on an Illumina MiSeq instrument with a MiSeq Reagent Kit v2 (500 cycles).

3.2.6 COI sequences determination

Raw Illumina MiSeq paired-end reads were processed using USEARCH v10.0.240 (Edgar, 2016-a, 2016-b) and VSEARCH 2.21.1 (Rognes *et al.*, 2016) commands (see supplementary materials 1). We used the mitochondrial cytochrome oxidase subunit 1 gene (COI) reference database acquired from The Barcode of Life Data System BOLD (O'Rourke *et al.*, 2020; Robeson *et al.*, 2021). Only the ASVs with a number of sequences greater than 10 were retained and considered as present, while they were considered absent under 10 reads. All the ASVs that were identified to the family with a confidence above 0.8 were then retained. We then created a matrix that represented the taxonomic diversity of each family by counting every unique ASVs for each family on each plot.

3.2.7 Statistical analyses

3.2.7.1 Objective 1: Litter decomposition rate

The decomposition rate was calculated on the basis of the negative exponential model $M_t = M_0 e^{-kt}$ (Olson, 1963) where *M* is the mass of the dry litter, *t* is the time, and *k* is the constant decomposition rate. To obtain *k*, we calculated the value of the slope of the logarithmically transformed mass over time (in days) (Wang *et al.*, 2014). We realized eight linear models, one per sampling area, to determine the decomposition rate (*k*) of the litter from each.

The time variable value was calculated as the total number of days the decomposition bags remained in the sampling areas, from which 163 days were subtracted, which is the number of days that were estimated to have little or no decomposition during the winter. The first day of this period was set to November 13 because it was the first date at which air temperature never returned above 0° C for several consecutive days, and similarly the last day of this period was set to April 24, the first date when the air temperature never returned below 0° C for several consecutive days. All temperatures were extracted from https://climat.meteo.gc.ca/ using the climate station nearest to the park, which is Gatineau's airport, 35km away from the park.

We then calculated the Spearman correlation value between the eight decomposition rates and the percentage of ash leaves composing the litter in the decomposition bags to assess if decomposition rate was positively associated with the percentage of ash leaves.

3.2.7.2 Objective 2: Invertebrate diversity and community composition

For this objective, we assessed how the extinction of ash trees might impact the invertebrate communities of the litter. First, we determined what effect the percentage of ash trees and the structure of the forest had on the number of families found inside each plot. Then we tried to assess which variables had an effect on taxonomic diversity of the communities of invertebrates in the forest of Plaisance National Park.

The number of invertebrate families found in each plot (family richness) was analysed with a mixed linear model (normal distribution) including two explanatory variables: the percentage of ash basal area in the plot and the category of the plot (cut, adjacent or control, hereafter called collectively the treatments), and the site as a ramdom effect. Because pitfall traps were often disturbed (49% of the pitfall traps were disturbed at least once during the sampling period, representing in total 18% of the pitfall dates that were not sampled) during the summer, the logarithm of the number of trapping days was included as an offset variable to correct the number of families observed on each plot with the number of days of sampling. All models were run with the glmmTMB function from the glmmTMB package.

To determine the effects of the disappearance of ash spp. on the taxonomic diversity of invertebrate communities, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) and Permutational Analysis of Multivariate Dispersions (PERMDISP), respectively with the *adonis* and *permdisp* functions of the *vegan* package. We restricted the permutation within the eight different sites to take into account the spatial distribution of the 47 plots. PERMANOVA was used to test the difference in the assemblages between the treatments and along the ash gradient present across the eight sampling areas. The number of days of trapping was also included as a variable to account for the effect it could have on the number of ASVs detected. Since the PERMANOVA found a significant treatment effect, we realized the PERMDISP to test for homogeneity in multivariate dispersion. A significant result would indicate that the difference in the assemblages between the treatments is the result of a greater heterogeneity of one of the treatments, while a non-significant result indicates that the PERMANOVA is the evidence for distinct compositional patterns between treatments. We then used a principal coordinates ordination plot (with 80% confidence ellipses) to visualize the differences in composition between the 3 treatments.

Finally, to determine which environmental variable were driving the taxonomic diversity of each family, we realized a redundancy analysis (RDA). Prior to the analysis, the invertebrate matrix was Hellinger-transformed, which allowed to maintain the distance among sites and underweight rare taxa (Legendre & Gallagher, 2001). We tested several environmental variables in that RDA using the Bray-Curtis dissimilarity, which allows a linear response to the modification of the abundance of a taxa between plots (Ricotta & Podani, 2017). *(1) structure variables:* the basal area of dead standing trees, the canopy openness, the treatment, the quantity of coarse woody debris averaged between the four pitfall traps of the plot, and the percentage of cover averaged between the four pitfall traps of the plot; all measured for each plot. *(2) litter variable*: we also tested the decomposition rate measured on each site to assess the effect of the modification of the litter. We tested the significance of each variable and created a final RDA that only included the significant variables.

3.3 Results

3.3.1 Litter decomposition rate

The dry mass of the litter from the decomposition bags in each sampling area declined with time which allowed us to estimate the decomposition rate; *k* (Table 3.1). The correlation between the decomposition rate and the percentage of ash litter a significantly highwas positive (Spearman correlation coefficient of 0.79;p = 0.028) (Figure 3.2).

Table 3.1 Parameter estimates (*k* value), t and p values of the model explaining the logarithm of the litter mass with time (in days) for each of the eight sampling areas in Plaisance National Park, and the percentage of ash spp. litter that was determined for each plot.

	ash litter	Estimate of *k*	t value	p value
Site 1	49%	-0.007	-13.02	< 0.001
Site 2	26%	-0.009	-12.41	< 0.001
Site 3	47%	-0.006	-9.81	< 0.001
Site 4	68%	-0.011	-10.08	< 0.001
Site 5	15%	-0.004	-6.87	< 0.001
Site 6	36%	-0.005	-9.05	< 0.001
Site 7	17%	-0.004	-7.93	< 0.001
Site 8	15%	-0.004	-18.95	< 0.001

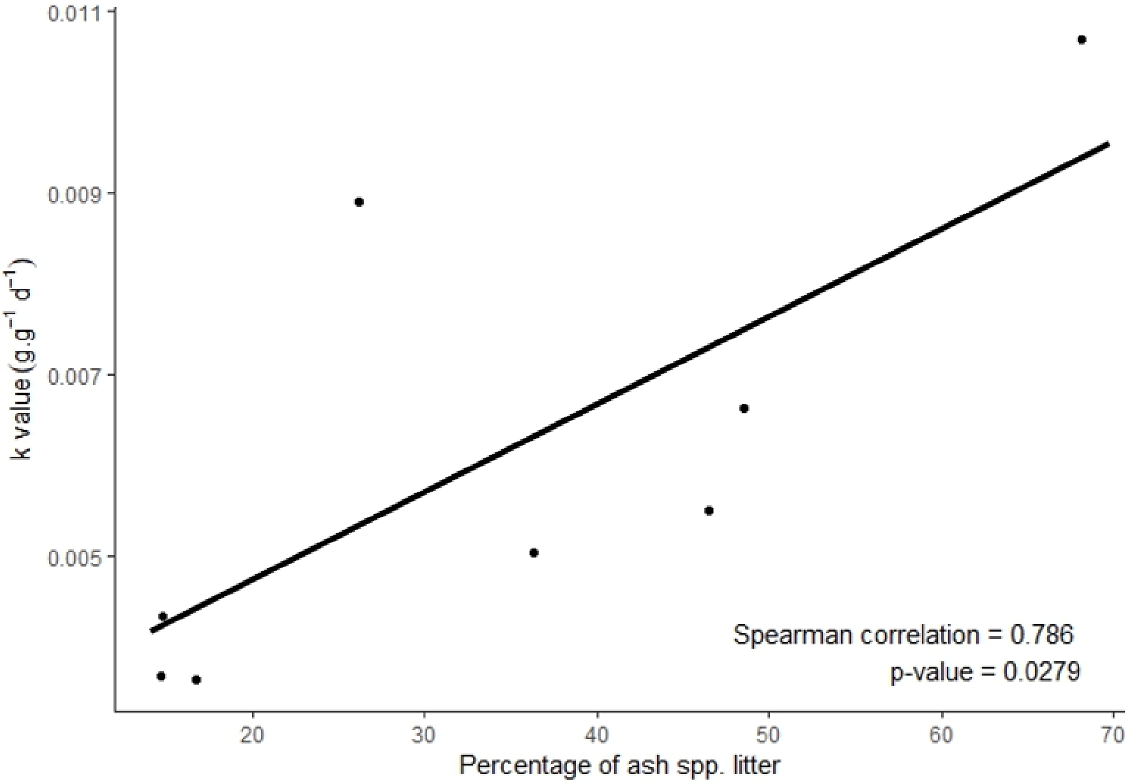

Figure 3.2 Spearman correlation between the decomposition rate (k value) of each sampling area in Plaisance National Park and the percentage of ash in its litter.

3.3.2 Family richness

In total, 71 invertebrate families from seven class were detected in this study (*Insecta*: 42, *Arachnida*: 18, *Collembola*: 6, *Gastropoda*: 2, *Chilopoda*: 1, *Clitellata*: 1 and *Malacostraca*: 1). Over the 3219 ASV units retained in this study, 1685 (53%) were from *Insecta*¸ 963 from *Collembola* (30%) and 375 from *Arachnida* (11%). Both the treatment and the percentage of ash spp had a significant effect on the number of invertebrate families found in each plot (Table 3.2). The control plots had significantly more families than the cut plot (average of 27.0 families in the control plots when there was no ash trees, and 21.5 in the cut plots in the same conditions). The percentage of ash spp. in each plot also appeared to have a slight negative, but significant effect on the abundance of families found in the plots (-0.05 taxa per percentage unit) (Table 3.2).

Table 3.2 Parameter estimate, z value and p value of the mixed model predicting the richness of ground dwelling invertebrates' families with the percentage of ash spp. in the basal area and the treatment (cut, adjacent and control plots) for the 47 plots sampled in Plaisance National Park. Significant results are shown in bold.

	Estimate	z value	p value
Intercept	**26.909**	**14.907**	**< 0.001**
Adjacent plots	**-3.301**	**-2.086**	**0.037**
Cut plots	**-5.445**	**-2.496**	**0.013**
Percentage of ash spp.	**-0.051**	**-2.048**	**0.041**

3.3.3 Invertebrate community composition

The assemblage of invertebrate families at the taxonomic diversity level significantly differed among the treatments and along the ash basal area gradient as evidenced from the PERMANOVA (Table 3.3). The PERMDISP results were not significant ($F_{2,44} = 0.04$; $p = 0.96$) indicating that there were no dispersion differences between the communities in the different treatments. The different treatment appeared to present some differences of community composition between control and cut plots (Figure 3.3).

Table 3.3 Results of PERMANOVA analysis of the taxonomic diversity of communities of invertebrates, at the family level. Significant variables are highlighted in bold.

	Df	SS	MS	F	p value
Treatment	**2**	**0.385**	**0.192**	**1.515**	**0.024**
Percentage of ash spp.	**1**	**0.296**	**0.296**	**2.332**	**0.025**
Days of trapping	1	0.282	0.282	2.224	0.249
Residuals	42	5.331	0.127		
Total	46	6.293			

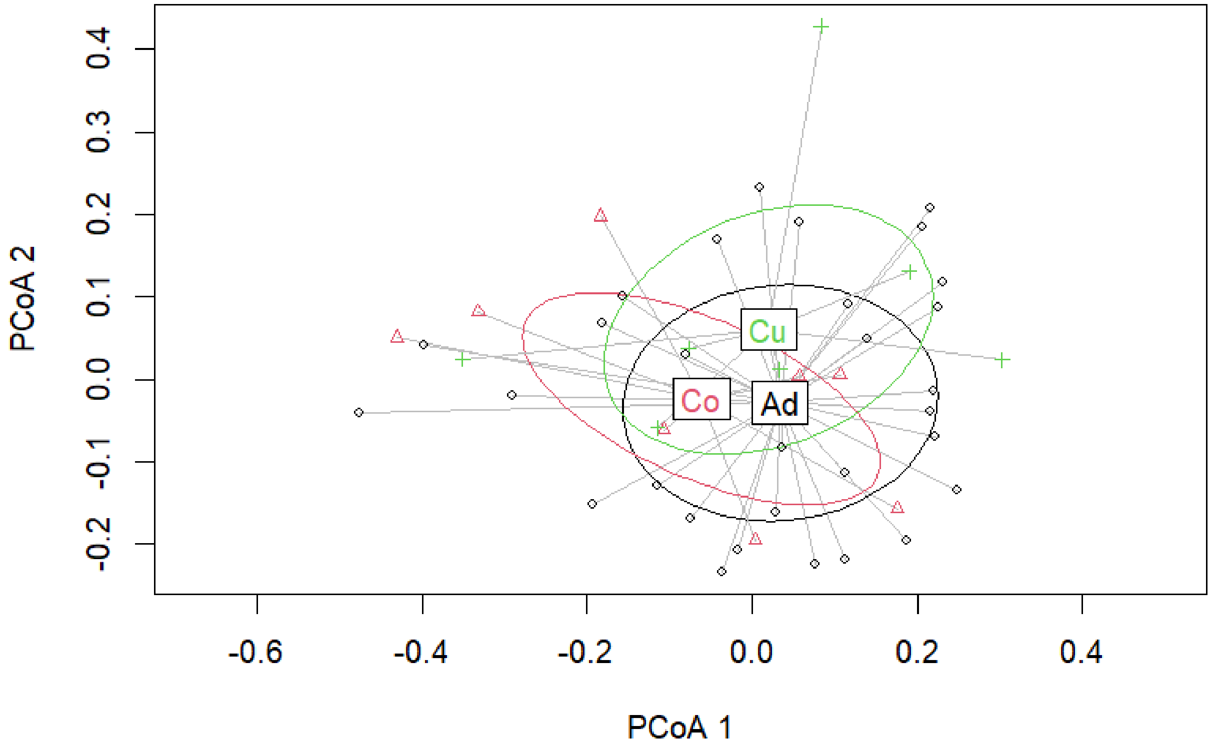

Figure 3.3 Ordination plot of the principal coordinates analyses (based on dissimilarity matrices calculated from Bray-Curtis dissimilarity index) representing dissimilarity in taxonomic diversity assemblage patterns among the cut plots (Cu), the adjacent plots (Ad) and the control plots (Co) for the ground dwelling invertebrate communities of the Plaisance National Park riparian forests. Green crosses are the cut plots, red triangles are the control plots and black circles are the adjacent plots.

The RDA (Figure 3.4) showed that invertebrate taxonomic diversity was significantly correlated with three of the tested variables: the canopy openness, the herbaceous cover, and the decomposition rate ($F = 2.31$, $p = 0.001$). The model explained 14% of the variance in the family data (first axis: 8%, second axis: 5%) with an adjusted R^2 of 8%. The first axis was positively correlated to the rate of decomposition calculated for each site. The second axis was negatively correlated with the two structure variables: the canopy openness, and the herbaceous cover. Most of the families were not impacted by the variables at the taxonomic diversity level, but some insects, collembola and arachnida were. Cicadellidae, Katiannidae, Miridae, Chironomidae and Dicyrtomidae taxonomic diversity was associated with a high decomposition rate, while

Trigonidiidae, Tomoceridae, Lampyridae and Elateridae taxonomic diversity was associated with low decomposition rates (Axis 1, Figure 3.4). Tomoceridae, Rhaphidophoridae, Katiannidae, Chironomidae, Haplozetidae, Sclerosomatidae and Galumnidae were also associated with low values of canopy openness and herbaceous cover (axis 2, Figure 3.4). Finally, Elateridae, Dicyrtomidae and Trigonidiidae taxonomic diversity increased with high canopy openness, herbaceous cover, and ash basal area (axis 2, Figure 3.4).

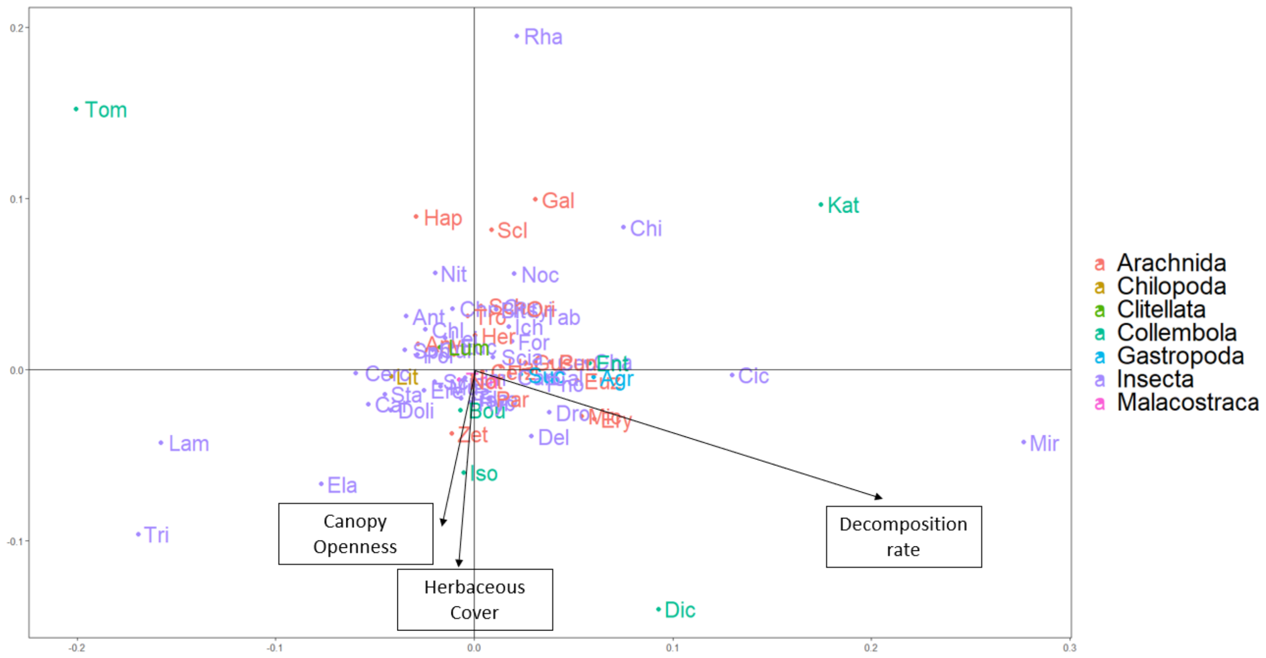

Figure 3.4 RDA ordination of invertebrate taxonomic diversity explained through the average percentage of ash spp. basal area, the decomposition rate of each site, the canopy openness, and the average herbaceous cover. Different classes of invertebrates appear in different colours. The list of the abbreviations for the name of the families is given in supplementary material 2.

3.4 Discussion

This study aimed to better understand how invertebrate communities could potentially be altered by the invasion of the EAB, which will cause the mortality of nearly all ash trees in riparian forests of temperate forests. In this study, we found that the rate of litter decomposition in riparian forests was partially driven by the proportion of ash leaves in the litter (Obj. 1). Furthermore, we were able to show that invertebrate communities were likely to be altered, both by structural changes in the forest and litter change (Obj. 2).

The effect of the ash disappearance has already been studied on communities of invertebrates, however, mainly by focusing on the modification of forest structure, canopy openness and coarse woody debris dynamics' (Perry, Wallin, *et al.*, 2018; Perry & Herms, 2016b; Ulyshen *et al.*, 2011). Although the effects of the disappearance of a high-quality litter on invertebrates have been suggested (Nisbet *et al.*, 2015), it has only been tested on aquatic invertebrates so far (Kreutzweiser *et al.*, 2019). To our knowledge, the decomposition rate has never been compared between litters dominated either by ash (mainly *Fxaxinus americana*) or maple (mainly *Acer saccharinum*). Our results showed that the decomposition rate increased with the percentage of ash leaves composing the litter, which is consistent with the literature. Indeed, litter with leaves of ash spp. is often reported to have a faster decomposition rate than litter of maple spp. (Jacob *et al.*, 2010a; Palik *et al.*, 2005).

Some invertebrate families were influenced by the structure of the forest (canopy openness and herbaceous cover) and by the litter decomposition rate as revealed by the RDA. Most of the families did not appear to be influenced by any of the variables tested in the RDA, which can be the reflect of either a low taxonomic diversity of the families in question, their ubiquity, their rarity, or that the variable tested were actually not important for the taxonomic diversity of these families. Regarding the families that were related to the tested variables, it is likely that the effect of the disappearance of ash trees will depend on the family, but it appears that species in the families of Rhaphidophoridae, Katiannidae and Chironomidae will be impacted negatively since their taxonomic diversity is negatively impacted by canopy openness and herbaceous cover, and positively impacted by the decomposition rate of the litter.

The three families of collembola that responded to the different explanatory variables will likely react differently to the extinction of ash trees. Katiannidaes will, as mentioned, be influenced negatively by both the modification of the canopy structure and the modification of the litter quality. Dicyrtomidaes might be positively influenced by the modification of canopy structure of the forest at first, but will be negatively influenced by the decreasing decomposition rate of the litter. On the other hand, Tomoceridae taxonomic diversity might decrease at first, with the increased of canopy openness and an increase in herbaceous cover, but will benefit from the reduction of the decomposition rate afterwards. These three collembola families have a relatively similar taxonomic diversity in Canada, since Katiannidae, Tomoceridae and Dicyrtomidae are represented respectively by 10, 12 and 8 species in Canada, respectively represented by 87, 70 and 78 Barcodes Index Numbers (Turnbull & Stebaeva, 2019). Collembola are known for their critical role in the ecology of the soil (Rusek, 1998). Katiannidae and Tomoceridae which are epedaphic, and Dicyrtomidae which are atmobiotic (Potapov *et al.*, 2016) might have an important role for the soil structuration and for the early decomposition stage. Modifications in the communities of collembola could potentially result in even greater modifications of the habitat, and while the present study does not allow to predict what those changes might be, it highlights the need for further studies on that subject. Indeed, some studies demonstrated that there should not be any changes in soil nutrients cycling after the invasion of the EAB in the long term, or that the changes should be minimal (Kreutzweiser *et al.*, 2020; Matthes *et al.*, 2018; Sibley *et al.*, 2020). On the other hand, other studies showed that the changes in the soil composition could have important consequences on soil processes (Davis *et al.*, 2019). It could therefore be interesting to pursue further studies on the effect of the extinction of ash trees, on soil microbial and fungal communities in order to assess how they could affect soil nutrient cycling processes given their known role as such (Burke *et al.*, 2011; Fernandez *et al.*, 2016; Li *et al.*, 2022).

Instinctively, one might think that more precise results could be obtained if all ASVs were attributed to a species instead of a family. However, some ASVs, especially for invertebrate taxa, cannot be assigned at the species level, either because databases are incomplete or because the species in question is not yet known as for its genetic structure (van der Heyde *et al.*, 2021). Many studies therefore choose to conduct their analyses at the family level rather than at the species or genera levels because this allows a greater number of reads to be identified and because the conclusions are similar for all taxonomic levels in studies that tested the species, the genus, and the family levels (Buss & Vitorino, 2010; Hewlett, 2000; Marshall *et al.*, 2006; Waite *et al.*, 2004).

Because of the small size of the cut plot, and because invertebrates were sampled only one year after the cut, it is very likely that the intensity of the effect of cutting dead ashes was underestimated in this study. However, the fact that we were still able to detect differences in the number of families and in their taxonomic diversity clearly points toward the idea that the invasion of the EAB will impact the invertebrate communities due to the modification of the forest structure and of the litter resulting from ash tree mortality. Still, it is to be noted that despite the different effects that the disappearance of ash trees will have on the biodiversity of the ground dwelling invertebrates, our study does not allow to determine if those modifications will have an effect on ecological functions such as the rate of decomposition of the litter in previously ash-dominated riparian forests.

Ideally, a Before-After Control-Impact (BACI) design would have been better suited for our objectives. However, one thing that was not possible to control was the rate at which the ash-dominated forest in the park would die from EAB invasion. The presence of the insect was first officially detected in 2016. It was urgent to install the cut plots so to not have the EAB interfere with the experimental design. Alternatively, the option of starting the sampling effort before EAB cause sufficient mortality to implement an after-sampling period was fraught with uncertainty. Hence, the implemented design was considered as a trade-off and even more informative by including the effect of another dominant tree genera, the maples, and the impact of its disappearance on the invertebrate communities in the habitat they generate. It is hoped that the results of the present study stimulate further studies on the dynamics of nutrients in such crucial environments as riparian forests. There are a multitude of studies on the role of these environments as subsidies provider to the adjacent aquatic habitats, but very little on the importance of litter turnover on riparian forest productivity *per se*.

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3.5 References

Aljanabi, S. M., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. In Nucleic Acids Research (Vol. 25, Issue 22). Oxford University Press.

Aulen, M., Shipley, B., & Bradley, R. (2012). Prediction of in situ root decomposition rates in an interspecific context from chemical and morphological traits. Annals of Botany, 109(1), 287–297. https://doi.org/10.1093/aob/mcr259

Beng, K. C., Tomlinson, K. W., Shen, X. H., Surget-Groba, Y., Hughes, A. C., Corlett, R. T., & Slik, J. W. F. (2016). The utility of DNA metabarcoding for studying the response of arthropod diversity and composition to land-use change in the tropics. Scientific Reports, 6. https://doi.org/10.1038/srep24965

Blaxter, M. L. (2004). The promise of a DNA taxonomy. In Philosophical Transactions of the Royal Society B: Biological Sciences (Vol. 359, Issue 1444, pp. 669–679). Royal Society. https://doi.org/10.1098/rstb.2003.1447

Burke, D. J., Weintraub, M. N., Hewins, C. R., & Kalisz, S. (2011). Relationship between soil enzyme activities, nutrient cycling and soil fungal communities in a northern hardwood forest. Soil Biology and Biochemistry, 43(4), 795–803. https://doi.org/10.1016/j.soilbio.2010.12.014

Buss, D. F., & Vitorino, A. S. (2010). Rapid Bioassessment Protocols using benthic macroinvertebrates in Brazil: Evaluation of taxonomic sufficiency. Journal of the North American Benthological Society, 29(2), 562–571. https://doi.org/10.1899/09-095.1

Černecká, Ľ., Mihál, I., Gajdoš, P., & Jarčuška, B. (2020). The effect of canopy openness of European beech (Fagus sylvatica) forests on ground-dwelling spider communities. Insect Conservation and Diversity, 13(3), 250–261. https://doi.org/10.1111/icad.12380

Collier, K. J., Bury, S., & Gibbs, M. (2002). A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshwater Biology, 47(9), 1651–1659. https://doi.org/10.1046/j.1365-2427.2002.00903.x

Davis, J. C., Shannon, J. P., Van Grinsven, M. J., Bolton, N. W., Wagenbrenner, J. W., Kolka, R. K., & Pypker, T. G. (2019). Nitrogen cycling responses to simulated emerald ash borer infestation in *Fraxinus* nigra-dominated wetlands. Biogeochemistry, 145(3), 275–294. https://doi.org/10.1007/s10533-019-00604-2

de Vries, P. G. (1973). A general theory on line intersect sampling with application to logging residue inventory.

Edgar, R. C. (2016-a). SINTAX: a simple non-Bayesian taxonomy classifier for 16S and ITS sequences. https://doi.org/10.1101/074161

Edgar, R. C. (2016-b). UNOISE2: improved error-correction for Illumina 16S and ITS amplicon sequencing. https://doi.org/10.1101/081257

Engelken, P. J., & McCullough, D. G. (2020). Riparian forest conditions along three northern Michigan rivers following emerald ash borer invasion. Canadian Journal of Forest Research, 50(8), 800–810. https://doi.org/10.1139/cjfr-2019-0387

Fernandez, A. L., Sheaffer, C. C., Wyse, D. L., Staley, C., Gould, T. J., & Sadowsky, M. J. (2016). Associations between soil bacterial community structure and nutrient cycling functions in long-term organic farm soils following cover crop and organic fertilizer amendment. Science of the Total Environment, 566–567, 949–959. https://doi.org/10.1016/j.scitotenv.2016.05.073

Forio, M. A. E., de Troyer, N., Lock, K., Witing, F., Baert, L., de Saeyer, N., Rîșnoveanu, G., Popescu, C., Burdon, F. J., Kupilas, B., Friberg, N., Boets, P., Volk, M., McKie, B. G., & Goethals, P. (2020). Small patches of riparian woody vegetation enhance biodiversity of invertebrates. Water (Switzerland), 12(11), 1–21. https://doi.org/10.3390/w12113070

Gandhi, K. J. K., & Herms, D. A. (2010). North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien Emerald ash borer. Biological Invasions, 12(6), 1839–1846. https://doi.org/10.1007/s10530-009-9594-1

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. https://doi.org/10.1007/s10841-013-9565-9

Gregory, S. v, Swanson, F. J., McKee, W. A., & Cummins, K. W. (1991). An Ecosystem Perspective of Riparian Zones. BioScience, 41(8), 540–551. http://www.jstor.org/action/showPublisher?publisherCode=aibs.

Grinde, A. R., Youngquist, M. B., Slesak, R. A., Kolbe, S. R., Bednar, J. D., Palik, B. J., & D’Amato, A. W. (2022). Potential impacts of emerald ash borer and adaptation strategies on wildlife communities in black ash wetlands. Ecological Applications. https://doi.org/10.1002/eap.2567

Grodsky, S. M., Moorman, C. E., Fritts, S. R., Campbell, J. W., Sorenson, C. E., Bertone, M. A., Castleberry, S. B., & Wigley, T. B. (2018). Invertebrate community response to coarse woody debris removal for bioenergy production from intensively managed forests. Ecological Applications, 28(1), 135–148. https://doi.org/10.1002/eap.1634

Harmon, M. E., & Sexton, J. (1996). Guidelines for Measurements of Woody Detritus in Forest Guidelines for Measurements of Woody Detritus in Forest Ecosystems Ecosystems. https://digitalrepository.unm.edu/lter_reports

Hättenschwiler, S., Tiunov, A. v., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. In Annual Review of Ecology, Evolution, and Systematics (Vol. 36, pp. 191–218). https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hewlett, R. (2000). Implications of taxonomic resolution and sample habitat for stream classification at a broad geographic scale. In Am. Benthol. Soc (Vol. 19, Issue 2).

Hunter, M. L., Acuña, V., Bauer, D. M., Bell, K. P., Calhoun, A. J. K., Felipe-Lucia, M. R., Fitzsimons, J. A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C. J., Medellin, R. A., Nelson, E. J., & Poschlod, P. (2017). Conserving small natural features with large ecological roles: A synthetic overview. Biological Conservation, 211, 88–95. https://doi.org/10.1016/j.biocon.2016.12.020

Jacob, M., Viedenz, K., Polle, A., & Thomas, F. M. (2010). Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (Fagus sylvatica). Oecologia, 164(4), 1083–1094. https://doi.org/10.1007/s00442-010-1699-9

Ji, Y., Ashton, L., Pedley, S. M., Edwards, D. P., Tang, Y., Nakamura, A., Kitching, R., Dolman, P. M., Woodcock, P., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., Hamer, K. C., Wilcove, D. S., Bruce, C., Wang, X., Levi, T., Lott, M., … Yu, D. W. (2013). Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. Ecology Letters, 16(10), 1245–1257. https://doi.org/10.1111/ele.12162

Jonczak, J. (2009). Leaf litter fall decomposition in age-differentiated stands of poplar clone Hybrid 275. Polish Journal of Soil Science, 42(2), 159–166. https://www.researchgate.net/publication/273945069

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P., & Lepage, M. (2006). Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. In Applied Soil Ecology (Vol. 32, Issue 2, pp. 153–164). https://doi.org/10.1016/j.apsoil.2005.07.004

Kelemen, K., Mihók, B., Gálhidy, L., & Standovár, T. (2012). Dynamic response of herbaceous vegetation to gap opening in a central European beech stand. Silva Fennica, 46(1), 53–65. https://doi.org/10.14214/sf.65

Knight, K. S., Brown, J. P., & Long, R. P. (2013). Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (Agrilus planipennis). Biological Invasions, 15(2), 371–383. https://doi.org/10.1007/s10530-012-0292-z

Koivula, M., Punttila, P., Haila, Y., & Nicnielii Koivula Punltila P-, J. M. (1999). Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest.

Kreutzweiser, D., Dutkiewicz, D., Capell, S., Sibley, P., & Scarr, T. (2020). Changes in streamside riparian forest canopy and leaf litter nutrient flux to soils during an emerald ash borer infestation in an agricultural landscape. Biological Invasions, 22(6), 1865–1878. https://doi.org/10.1007/s10530-020-02223-7

Laird-Hopkins, B. C., Bréchet, L. M., Trujillo, B. C., & Sayer, E. J. (2017). Tree functional diversity affects litter decomposition and arthropod community composition in a tropical forest. Biotropica, 49(6), 903–911. https://doi.org/10.1111/btp.12477

Lasota, J., Piaszczyk, W., & Błońska, E. (2022). Fine woody debris as a biogen reservoir in forest ecosystems. In Acta Oecologica (Vol. 115). Elsevier B.V. https://doi.org/10.1016/j.actao.2022.103822

Lecerf, A., & Chauvet, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. Basic and Applied Ecology, 9(5), 598–605. https://doi.org/10.1016/j.baae.2007.11.003

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. Oecologia, 129(2), 271–280. https://doi.org/10.1007/s004420100716

Leroy, C. J., Whitham, T. G., Wooley, S. C., & Marks, J. C. (2007). Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. In Am. Benthol. Soc (Vol. 26, Issue 3).

Li, X., Qu, Z., Zhang, Y., Ge, Y., & Sun, H. (2022). Soil Fungal Community and Potential Function in Different Forest Ecosystems. In Diversity (Vol. 14, Issue 7). MDPI. https://doi.org/10.3390/d14070520

Maisonneuve, C., & Rioux, S. (2001). Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Québec. Ecosystems and Environment, 83, 165–175.

Marshall, J. C., Steward, A. L., & Harch, B. D. (2006). Taxonomic resolution and quantification of freshwater macroinvertebrate samples from an Australian dryland river: The benefits and costs of using species abundance data. Hydrobiologia, 572(1), 171–194. https://doi.org/10.1007/s10750-005-9007-0

Matthes, J. H., Lang, A. K., Jevon, F. V., & Russell, S. J. (2018). Tree stress and mortality from emerald ash borer does not systematically alter short-term soil carbon flux in a mixed northeastern U.S. forest. Forests, 9(1). https://doi.org/10.3390/f9010037

Murakami, M., & Nakano, S. (2001). Species-specific foraging behavior of birds in a riparian forest. Ecological Research, 16, 913–923.

Naiman, R. J., & Decamps, H. (1997). The Ecology Of Interfaces-Riparian Zones. Annual Review of Ecology and Systematics, 621–658.

O’Brien, P. A., Tan, S., Yang, C., Frade, P. R., Andreakis, N., Smith, H. A., Miller, D. J., Webster, N. S., Zhang, G., & Bourne, D. G. (2020). Diverse coral reef invertebrates exhibit patterns of phylosymbiosis. ISME Journal, 14(9), 2211–2222. https://doi.org/10.1038/s41396-020-0671-x

Olson, J. S. (1963). Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. Ecology, 44(2), 322–331.

Paine, L. K., & Ribic, C. A. (2002). Comparison of riparian plant communities under four land management systems in southwestern Wisconsin. Ecosystems and Environment, 92, 93–105.

Palik, B., Batzer, D. P., & Kern, C. (2005). Upland Forest Linkages to Seasonal Wetlands: Litter lux, Processing, and Food Quality. Ecosystems, 8, 1–11. https://doi.org/10.10071~1002

Perry, K. I., Herms, D. A., Klooster, W. S., Smith, A., Hartzler, D. M., Coyle, D. R., & Gandhi, K. J. K. (2018). Downed coarse woody debris dynamics in ash (*Fraxinus* spp.) stands invaded by emerald ash borer (Agrilus planipennis Fairmaire). Forests, 9(4). https://doi.org/10.3390/f9040191

Perry, K. I., Wallin, K. F., Wenzel, J. W., & Herms, D. A. (2018). Forest disturbance and arthropods: Small-scale canopy gaps drive invertebrate community structure and composition. Ecosphere, 9(10). https://doi.org/10.1002/ecs2.2463

Potapov, A. A., Semenina, E. E., Korotkevich, A. Y., Kuznetsova, N. A., & Tiunov, A. V. (2016). Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms. Soil Biology and Biochemistry, 101, 20–31. https://doi.org/10.1016/j.soilbio.2016.07.002

Ramey, T. L., & Richardson, J. S. (2017). Terrestrial Invertebrates in the Riparian Zone: Mechanisms Underlying Their Unique Diversity. In BioScience (Vol. 67, Issue 9, pp. 808–819). Oxford University Press. https://doi.org/10.1093/biosci/bix078

Ricotta, C., & Podani, J. (2017). On some properties of the Bray-Curtis dissimilarity and their ecological meaning. *Ecological Complexity*, *31*, 201-205.

Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. PeerJ, 2016(10). https://doi.org/10.7717/peerj.2584

Rosner, S., Dupuch, A., & Lorenzetti, F. (2022). Stuck between the mandibles of an insect and of a rodent: where does the fate of ash-dominated riparian temperate forests lie? Forests, 13(11), 1760. https://doi.org/10.3390/f13111760

Rusek, J. (1998). Biodiversity of Collembola and their functional role in the ecosystem. Biodiversity and Conservation, 7, 1207–1219. https://doi.org/10.1023/A:1008887817883

Sayer, E. J., Sutcliffe, L. M. E., Ross, R. I. C., & Tanner, E. V. J. (2010). Arthropod abundance and diversity in a lowland tropical forest floor in Panama: The role of habitat space vs. nutrient concentrations. Biotropica, 42(2), 194–200. https://doi.org/10.1111/j.1744-7429.2009.00576.x

Sibley, P. K., Dutkiewicz, D., Kreutzweiser, D. P., & Hazlett, P. (2020). Soil and nutrient cycling responses in riparian forests to the loss of Ash (*Fraxinus* spp. L) from Emerald Ash Borer (Agrilus planipennis, Fairmaire). Forests, 11(5). https://doi.org/10.3390/F11050489

Siegert, N. W., Mccullough, D. G., Liebhold, A. M., & Telewski, F. W. (2014). Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. Diversity and Distributions, 20(7), 847–858. https://doi.org/10.1111/ddi.12212

Steyaert, M., Priestley, V., Osborne, O., Herraiz, A., Arnold, R., & Savolainen, V. (2020). Advances in metabarcoding techniques bring us closer to reliable monitoring of the marine benthos. Journal of Applied Ecology, 57(11), 2234–2245. https://doi.org/10.1111/1365-2664.13729

Ulyshen, M. D. (2016). Wood decomposition as influenced by invertebrates. Biological Reviews, 91(1), 70–85. https://doi.org/10.1111/brv.12158

van der Heyde, M., Bunce, M., Dixon, K., Fernandes, K., Majer, J., Wardell-Johnson, G., White, N., Nevill, P., & der Heyde, van. (2021). Evaluating restoration trajectories using DNA metabarcoding of invertebrates and their associated plant communities. Authorea Preprints. https://doi.org/10.22541/au.161383346.69785032/v1

Vauramo, S., & Setälä, H. (2011). Decomposition of labile and recalcitrant litter types under different plant communities in urban soils. Urban Ecosystems, 14(1), 59–70. https://doi.org/10.1007/s11252-010-0140-9

Waite, I. R., Herlihy, A. T., Larsen, D. P., Urquhart, N. S., & Klemm, D. J. (2004). The effects of macroinvertebrate taxonomic resolution in large landscape bioassessments: An example from the Mid-Atlantic Highlands, U.S.A. Freshwater Biology, 49(4), 474–489. https://doi.org/10.1111/j.1365-2427.2004.01197.x

Wang, X. Y., Miao, Y., Yu, S., Chen, X. Y., & Schmid, B. (2014). Genotypic diversity of an invasive plant species promotes litter decomposition and associated processes. Oecologia, 174(3), 993–1005. https://doi.org/10.1007/s00442-013-2816-3

Wipfli, M. S. (1997). Terrestrial invertebrates as salmonid prey andnitrogen sources in streams: contrastingold-growth and young-growth riparian forests insoutheastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences, 54, 1259–1269.

Xiong, Y., West, C. P., Brown, C. P., & Green, P. E. (2019). Digital image analysis of old world bluestem cover to estimate canopy development. Agronomy Journal, 111(3), 1247–1253. https://doi.org/10.2134/agronj2018.08.0502

3.6 Supplementary material

Supplementary material 1: list of commands used to obtain the matrix of ASVs

Mergepair

```
usearch -fastq_mergepairs reads/*R1.fastq -fastqout U-out/merged455.fq -relabel @ -fastq_maxdiffs 10 -fastq_pctid 80 -fastq_minmergelen 455 -fastq_maxmergelen 455 -report U-logs/mergeReport455.log
```

Remove primers and quality filter

```
Vsearch/bin/vsearch -fastx_filter U-out/merged455.fq -fastq_stripleft 26 -fastq_stripright 26 -fastq_maxee 1.0 -fastq_qmax 42 -fastaout U-out/stripped455.fa
```

Dereplication

```
Vsearch/bin/vsearch -derep_fulllength U-out/stripped455.fa -sizeout -relabel Uniq -output U-out/unique455.fa
```

Generate ASV

```
usearch -unoise3 U-out/unique455.fa -zotus ASV455a5.fa -minsize 4 -unoise_alpha 5 -tabbedout U-logs/denoise5.log
```

```
# Antich et al., 2021 confirmed that α = 5 in UNOISE3 is adequate for COI data, in line with previous research using three independent approaches. The default parameter is 2 (ribosomal markers).
```

Table ASV

```
Vsearch/bin/vsearch -usearch_global U-out/stripped455.fa -db ASV455a5.fa -id 0.97 --otutabout ASV_countsa5.txt
```

Taxonomic attribution

```
Vsearch/bin/vsearch -sintax ASV455a5.fa -db database/COI1.fa -tabbedout ASV455a5.tax -sintax_cutoff 0.8 -strand plus
```

Supplementary material 2: list of the abbreviations used in the plot of the RDA (figure 3.4).

Abbreviation	Class	Order	Family
Agr	Gastropoda	Stylommatophora	Agriolimacidae
Ant	Insecta	Diptera	Anthomyiidae
Any	Arachnida	Acari	Anystidae
Bit	Insecta	Mecoptera	Bittacidae
Bou	Collembola	Symphypleona	Bourletiellidae
Cal	Insecta	Diptera	Calliphoridae
Can	Insecta	Coleoptera	Cantharidae
Car	Insecta	Coleoptera	Carabidae
Cec	Insecta	Diptera	Cecidomyiidae
Cerc	Insecta	Hemiptera	Ceratocombidae
Cerz	Arachnida	Oribatida	Ceratozetidae
Cha	Insecta	Diptera	Chaoboridae
Chi	Insecta	Diptera	Chironomidae
Chl	Insecta	Diptera	Chloropidae
Chr	Insecta	Coleoptera	Chrysomelidae
Cic	Insecta	Hemiptera	Cicadellidae
Cul	Insecta	Diptera	Culicidae
Cur	Insecta	Coleoptera	Curculionidae
Del	Insecta	Hemiptera	Delphacidae
Dic	Collembola	Symphypleona	Dicyrtomidae
Doli	Insecta	Diptera	Dolichopodidae
Dro	Insecta	Diptera	Drosophilidae
Ela	Insecta	Coleoptera	Elateridae
Ent	Collembola	Entomobryomorpha	Entomobryidae
Ere	Insecta	Lepidoptera	Erebidae
Ery	Arachnida	Trombidiformes	Erythraeidae
Euc	Insecta	Coleoptera	Eucnemidae
Euz	Arachnida	Oribatida	Euzetidae
Fla	Insecta	Hemiptera	Flatidae

Abbreviation	Class	Order	Family
For	Insecta	Hymenoptera	Formicidae
Gal	Arachnida	Oribatida	Galumnidae
Gus	Arachnida	Sarcoptiformes	Gustaviidae
Hal	Arachnida	Mesostigmata	Halolaelapidae
Hap	Arachnida	Oribatida	Haplozetidae
Her	Arachnida	Sarcoptiformes	Hermanniellidae
Hyb	Insecta	Diptera	Hybotidae
Ich	Insecta	Hymenoptera	Ichneumonidae
Iso	Collembola	Entomobryomorpha	Isotomidae
Kat	Collembola	Symphypleona	Katiannidae
Lam	Insecta	Coleoptera	Lampyridae
Lei	Insecta	Coleoptera	Leiodidae
Lim	Insecta	Diptera	Limoniidae
Lit	Chilopoda	Lithobiomorpha	Lithobiidae
Lum	Clitellata	Opisthopora	Lumbricidae
Mic	Arachnida	Trombidiformes	Microtrombidiidae
Mir	Insecta	Hemiptera	Miridae
Mus	Insecta	Diptera	Muscidae
Nit	Insecta	Coleoptera	Nitidulidae
Noc	Insecta	Lepidoptera	Noctuidae
Not	Arachnida	Oribatida	Nothridae
Ori	Arachnida	Oribatida	Oribatulidae
Par	Arachnida	Mesostigmata	Parasitidae
Pho	Insecta	Diptera	Phoridae
Pol	Insecta	Diptera	Polleniidae
Psyi	Insecta	Lepidoptera	Psychidae
Psyo	Insecta	Diptera	Psychodidae
Pun	Arachnida	Oribatida	Punctoribatidae
Rha	Insecta	Orthoptera	Rhaphidophoridae
Sch	Arachnida	Oribatida	Scheloribatidae
Scia	Insecta	Diptera	Sciaridae

Abbreviation	Class	Order	Family
Scio	Insecta	Diptera	Sciomyzidae
Scl	Arachnida	Opiliones	Sclerosomatidae
Sph	Insecta	Diptera	Sphaeroceridae
Sta	Insecta	Coleoptera	Staphylinidae
Suc	Gastropoda	Stylommatophora	Succineidae
Tab	Insecta	Diptera	Tabanidae
Tom	Collembola	Entomobryomorpha	Tomoceridae
Tra	Malacostraca	Isopoda	Trachelipodidae
Tri	Insecta	Orthoptera	Trigonidiidae
Tro	Arachnida	Trombidiformes	Trombidiidae
Zet	Arachnida	Oribatida	Zetomimidae

CHAPITRE 4
CONCLUSION

4.1 Importance du frêne pour la biodiversité des forêts ripariennes

Nous avons pu démontrer grâce à ces trois chapitres que les frênes jouent un rôle important pour le maintien de la biodiversité des forêts ripariennes dominées par celui-ci. En effet, nous avons pu mettre en évidence qu'il s'agit du genre taxinomique d'arbres le plus consommé par les castors, ce qui implique que les frênes peuvent être défavorisé par l'herbivorie exercée par le castor. Cependant, nous avons également démontré que la disparition du frêne peut avoir un effet négatif sur les densités de populations de castors, ce qui risque d'entrainer par ricochet des modifications supplémentaires sur la dynamique forestière en place. Enfin, il nous a été possible de montrer que la disparition subite des frênes allait entrainer des modifications des communautés d'invertébrés du sol, tant par la modification structurelle de la forêt liée à la mort des arbres, que par la modification du caractère labile de la litière.

Dans le premier chapitre de ce doctorat, nous avons montré que les frênes jouaient un rôle majeur dans le régime alimentaire du castor. En effet, les frênes étaient le genre d'arbres composant la plus grande part du régime alimentaire des castors, quel que soit le diamètre des tiges. Le charme de Caroline et les peupliers étaient les deux seuls genres ayant une plus grande probabilité de consommation que le frêne, mais leur abondance relative ne permettait pas de leur accorder la même importance. Enfin, nous avons montré que les gaules de charme pourraient voir leur probabilité de consommation augmenter en l'absence de frênes matures. Par ailleurs, si les gaules de frêne diminuaient en abondance, ou disparaissaient, il est possible que la probabilité de consommation des érables matures, et des gaules de tilleul et de charme puissent diminuer. Cependant, ce dernier effet pourrait en réalité être dû à un cas de compétition apparente. Le castor étant une espèce très sélective (Barnes & Dibble, 1988; Vorel *et al.*, 2015), le frêne permettrait donc aux essences minoritaires d'être très peu consommées dans les forêts dominées par ce genre. Il semblerait donc logique de penser que l'herbivorie qui était jusque-là exercée sur les frênes soit donc transférée sur d'autres essences, afin de parer à la disparition du frêne. Cependant, cela serait sans prendre en compte les résultats du second chapitre de ce doctorat.

En effet, nous avons pu mettre en évidence que les frênes avaient un effet significatif sur le nombre d'individus au sein des colonies de castors : plus la densité des frênes était importante sur le territoire défendu par la colonie, et plus le nombre d'individus composant l'unité familiale (taille du groupe) était important. Cette relation permet donc de penser que la disparition du frêne pourrait entrainer des diminutions dans la taille populations de castors, notamment sur le plan de la taille des groupes familiaux, ce qui devrait minimiser, au moins partiellement, les dommages que ceux-ci pourront causer à la forêt résiduelle. Par ailleurs, avec la disparition des frênes, le genre préféré le plus abondant dans ce type de forêt, la sélection des ressources alimentaires du castor va nécessairement être modifiée. La quantité totale de biomasse qui sera consommée par les castors va certainement diminuer si les densités de population diminuent. Cependant, il n'en reste pas moins que le changement dans leur sélection des ressources alimentaires a le potentiel de modifier la dynamique forestière qui était en place, notamment par la consommation d'essences qui étaient jusque-là évitées.

La biodiversité animale a également été étudiée ici à travers les communautés d'invertébrés du sol, qui sont à la base des réseaux trophiques «food webs» et dont des modifications sont susceptibles de se répercuter à la fois sur ses niveaux supérieurs (Huryn, 1998), mais également sur l'environnement, du fait des services écosystémiques que ces communautés peuvent jouer (Lavelle *et al.*, 2006). Ici, nous avons pu mettre en évidence que l'assemblage des communautés, et la diversité taxinomique des familles présentes étaient influencées d'une part par la modification structurelle de la forêt induite par l'ouverture du couvert forestier et d'autre part par la vitesse de décomposition de la litière. En effet, la mortalité des frênes engendrera nécessairement une augmentation de bois mort, mais aussi la création de trouées qui permettront le développement d'une végétation herbacée plus dense et plus diversifiée (Kelemen *et al.*, 2012) causée par une ouverture de la canopée plus importante (Gandhi *et al.*, 2014). Le chapitre 3 a pu mettre en lumière l'importance de ces deux dernières variables pour la diversité taxinomique de certaines familles d'invertébrés. Il a également pu être constaté que le nombre de taxons dans les parcelles coupées était inférieur au nombre de taxons des parcelles témoins. Ainsi, la création de trouées dans la forêt riparienne, aura pour effet immédiat de diminuer le nombre de familles d'invertébrés présentes, mais également d'affecter négativement la diversité taxinomique de certaines de ces familles d'invertébrés, diminuant ainsi la biodiversité. Par ailleurs, les effets de la disparition des frênes sur la biodiversité ne seront pas uniquement le fait de la modification structurelle de la forêt. Le chapitre 3 a également documenté que la vitesse de décomposition de la litière était en grande partie déterminée par la quantité de feuilles de frênes dans celle-ci, et que la vitesse de décomposition favorisait la diversité taxinomique de certaines familles d'invertébrés. Il est donc possible d'affirmer que non seulement la biodiversité animale sera modifiée lorsque les frênes disparaitront, mais également que certaines de ces modifications ne vont pas se résorber une fois que les trouées créées par l'agrile se résorberont. En effet, la plupart des genres d'arbres ont une litière ayant une vitesse de décomposition inférieure à celle des frênes (Palik *et al.*, 2005; Webster & Benfield, 1986). Plusieurs familles d'invertébrés, comme les Cicadellidae, Katiannidae, Miridae, Chironomidae et Dicyrtomidae, étaient fortement affectées par la vitesse de décomposition de la litière.

4.2 Avenir de la forêt riparienne

Du point de vue de la perturbation qui est créée par l'invasion de l'agrile, et de la disparition des frênes qui s'en suivra, il semble très improbable que les forêts atteignent une résilience au sens propre du terme, c'est-à-dire un retour à l'état stable initial de toutes les variables de celui-ci avant perturbation (Pimm, 1984; Van Meerbeek *et al.*, 2021). L'avenir des forêts ripariennes dominées par les frênes semble difficile à prévoir en se basant uniquement sur les résultats obtenus dans ce doctorat. Comme cela est expliqué au chapitre 1, il n'est pas encore certain que les frênes disparaissent entièrement, car les tiges les plus petites pourraient se maintenir dans le temps dépendamment de l'action du castor. Assumant que les frênes soient bel et bien voués à disparaitre, un grand nombre de paramètres restent encore à prendre en compte, notamment les essences qui remplaceront les frênes, pour être en mesure de prévoir le futur des forêts ripariennes à court et à long terme.

4.2.1 Court terme

À court terme, la question la plus importante pour déterminer l'avenir des frênes, et celui des forêts ripariennes, serait de déterminer la réponse fonctionnelle du castor face aux frênes, ce qui n'a pas été possible dans le chapitre 1. La réponse fonctionnelle est la variation du nombre de proies (ici les tiges) consommées par un prédateur (ici le castor) en fonction de la densité de ses proies dans le milieu par unité de temps (Holling, 1959). Du type de réponse fonctionnelle pourrait dépendre le futur des frênes dans les forêts ripariennes. En effet, en ce qui concerne les tiges < 9cm, il n'est pas encore certain que l'invasion de l'agrile entraine une modification importante du régime alimentaire du castor, car l'agrile ne s'attaque qu'aux frênes de plus de 2 ou 3 cm de diamètre (Aubin *et al.*, 2015). De plus, à la mort des arbres matures, ceux-ci produiront des rejets de souche dont les densités dépendront de la densité initiale d'arbres de frêne. Ainsi, les densités de castors ne devraient pas connaître de changements drastiques à court terme, car les rejets de frênes constitueront des ressources qui -comme démontré dans le premier chapitre- sont très appréciées par le castor, et auront la même distribution spatiale que les frênes matures. C'est lorsque les castors auront consommé la majorité de ces rejets de souche que la question de la réponse fonctionnelle se posera. Les deux réponses fonctionnelles potentielles seraient le type 2 et le type 3 (Fryxell *et al.*, 1994; Fryxell & Doucet, 1993). Le castor, comme d'autres herbivores, est généralement mentionné comme ayant une réponse fonctionnelle de type 2, qui a un effet déstabilisant sur les espèces consommées, car le pourcentage de proies consommées est maximal lorsque les proies sont à faible densité. Cependant, il a déjà été supposé que le castor pourrait exhiber une réponse fonctionnelle de type 3 pour les essences qu'il préfère. Cette réponse fonctionnelle, à l'inverse de la réponse fonctionnelle de type 2, a un effet stabilisant sur les relations proies-prédateurs, car passé un certain seuil, le pourcentage de proies consommées décroit à mesure que les densités de proies diminuent. Malgré les efforts mis en place, il n'a pas été possible d'établir si les castors exhibent une réponse fonctionnelle de type 2 ou de type 3 envers le frêne. Il est donc impossible d'anticiper si l'action des castors sera complémentaire à celle de l'agrile, c'est-à-dire si les castors consommeront les frênes laissés intacts par l'agrile (type 2), ou si au contraire, la sélection des castors pour le frêne diminuera à mesure que les densités de frêne diminueront (type 3). Cette dernière possibilité pourrait permettre aux frênes de ne pas disparaitre totalement, et de se maintenir grâce à des dynamiques de rejet de souche. Une dynamique de rejets de souche pourrait potentiellement minimiser les effets de la disparition des frênes mature sur les castors, car une part de leur ressource resterait intacte, si tant est que les castors avaient une réponse fonctionnelle de type 3 pour les gaules de frênes. Si cela était le cas, il resterait encore à déterminer si certains peuplements de frênes pourraient se rétablir partiellement (ce qui apparait improbable), ou si au contraire, ceux-ci se feraient attaquer par l'agrile régulièrement, au fur et à mesure qu'ils se régénèrent (Aubin *et al.*, 2015). Si le frêne est bel et bien voué à disparaitre, il semble alors que le futur des forêts ripariennes dépendra en partie des essences qui coloniseront les trouées laissées par l'agrile, et de l'effet de ces nouvelles essences sur les castors et les communautés d'invertébrés.

4.2.2 Long terme

Les essences d'arbres ayant le potentiel de coloniser les trouées laissées par l'agrile sont nombreuses, d'autant plus dans des forêts aussi hétérogènes que celles étudiées ici. Bien entendu, il est probable que dépendamment des essences présentes localement autour des trouées, la colonisation par de nouvelles essences ne soit pas identique dans tous les secteurs qui seront ravagés par l'agrile. Il est donc possible que ce soit l'ensemble de la forêt résiduelle qui remplacera le frêne, dans des proportions relativement semblables à celles qui seront en place à la disparition du frêne. Étant donné l'hétérogénéité de la forêt et la multitude de scénarios de colonisation des trouées qui pourraient être envisagés, il sera considéré ici uniquement deux scénarios possibles à la suite de la disparition des arbres de frêne (≥ 9 cm) : (1) le frêne sera remplacé en majorité par des essences appréciées par le castor (soit autant soit plus appréciées que le frêne) ; (2) le frêne sera remplacé en majorité par des essences qui ne sont généralement pas appréciées par le castor.

4.2.2.1 Remplacement par des essences sélectionnées par le castor

Un grand nombre d'essences peuvent être sélectionnées par le castor dépendamment de la composition générale de la forêt (Barnes & Dibble, 1988; Gallant *et al.*, 2004; Johnston & Naiman, 1990; Raffel *et al.*, 2009; Vorel *et al.*, 2015), mais selon la littérature, plusieurs genres peuvent être considérés comme plus sélectionnés que les autres. Bien sûr, les peupliers et les saules sont des genres préférés dans l'immense majorité des études (Hall, 1960; Smith & Tyers, 2012; Vorel *et al.*, 2015). Le charme, lorsque présent, est également particulièrement apprécié comme cela a été démontré dans le premier chapitre de ce doctorat, mais également dans d'autres études (Rossell *et al.*, 2014). Finalement, le chêne est potentiellement sélectionné au même niveau que le frêne, puisqu'il semblait avoir autant de probabilité de se faire consommer que le frêne au parc national de Plaisance, et parce que plusieurs études le mentionnent comme une essence très appréciée (Raffel *et al.*, 2009). Bien que généralement peu abondants dans les forêts ripariennes du bassin de l'Outaouais, ces quatre genres n'en restent pas moins présents. Ce scénario de colonisation pourrait théoriquement être observé dans certains peuplements, notamment pour le peuplier et le saule qui sont souvent considérés comme des espèces pionnières en particulier dans les forêts ripariennes (Ahn *et al.*, 2007; Amlin & Rood, 2002; Ireland *et al.*, 2014). Cependant, le peuplier faux-tremble, présent au Parc National de Plaisance et qui est l'essence favorite des castors, n'est pas une espèce qui considérée comme compétitive en forêt tempérée, et qui est bien plus souvent associée aux forêts boréales. La colonisation des peuplement par cette espèce en particulier si elle survenait, serait donc probablement très anecdotique.

Si ces essences remplaçaient la majorité des frênes, alors il semble cohérent de penser que celles-ci remplaceraient également le frêne dans le régime alimentaire du castor. Dans ce scénario, la probabilité de consommation des essences qui ne sont généralement pas appréciées par le castor ne devrait pas être modifiée de manière significative, dans la mesure où des essences particulièrement appréciées seront disponibles. Par ailleurs, il serait probable que la qualité de l'habitat du castor soit peu, ou pas altérée. Il a déjà été démontré que les essences favorites du castor avaient un effet sur les populations de celui-ci, que ce soit sur la densité des colonies (Bergman *et al.*, 2018; Smith & Tyers, 2012), sur le nombre d'individus à l'intérieur de chacune d'entre elles (Fryxell, 2001), ou sur le nombre de juvéniles présents (Smith, 1997). Remplacer le frêne par d'autres ressources de haute qualité serait donc le scénario pour lequel les populations de castors ne seraient en réalité que peu ou pas affectées, et potentiellement celui qui amènerait le moins de changements à la dynamique déjà existante entre les castors et la forêt riparienne.

Concernant les effets de ce scénario sur la biodiversité des invertébrés du sol, il est difficile de les prévoir sans avoir de vitesse de décomposition précise pour ces essences. Dans l'étude réalisée pour ce doctorat, le taux de décomposition (valeur de *k*) était >0.01 (jour^{-1}) pour le site contenant le plus de litière de frêne, et autour de 0.004 (jour^{-1}) pour les sites contenant le moins de litière de frêne. D'un point de vue général, le saule semble avoir une vitesse de décomposition relativement semblable à celle du peuplier (Chauvet, 1987). Leur vitesse de décomposition est inférieure à celle du frêne, et semble relativement équivalente à celle de l'érable (Madritch & Cardinale, 2007; Palik *et al.*, 2005; Petersen *et al.*, 1974). Une recolonisation des trouées par le chêne, un autre genre utilisé par les castors (Raffel *et al.*, 2009), représenterait sans aucun doute une diminution encore plus drastique de la vitesse de décomposition de la litière, puisque ce genre est connu pour avoir une vitesse de décomposition très faible, même par rapport à l'érable (Alexander & Arthur, 2014; Babl-Plauche *et al.*, 2022). En comparaison à une recolonisation par les saules et les peupliers, ce dernier scénario causerait donc des modifications bien plus importantes des communautés d'invertébrés du sol, en raison de la qualité de la litière qui en serait fortement et durablement affectée. Cependant, aux vues des résultats obtenus dans le troisième chapitre de cette thèse, il semble évident que même une colonisation des trouées par les peupliers et les saules engendrerait des répercussions sur la diversité taxinomique de certaines familles d'invertébrés.

4.2.2.2 Remplacement par des essences non sélectionnées

Beaucoup d'essences sont souvent décrites comme évitées par le castor dans les études. La principale d'entre-elles en forêts ripariennes dominées par les frênes est le genre *Acer*, plus précisément l'érable argenté (*Acer saccharinum*) et l'érable de Freeman (*Acer* × *freemanii)* (Barnes & Dibble, 1988; Rosner *et al.*, 2022). Ces deux espèces peuvent être très abondantes dans les forêts ripariennes, et peuvent également être considérées comme des espèces pionnières (Ahn *et al.*, 2007). Du fait de leur forte abondance et de leur tolérance pour les sols inondés, il est envisageable que de grandes portions de la forêt en zone riparienne, décimée par l'agrile du frêne, soient colonisées par ces essences. Les tilleuls peuvent aussi représenter une proportion non négligeable des forêts ripariennes. Bien qu'ils semblent des candidats moins probables pour le remplacement des frênes des forêts ripariennes, ils causeraient sur les castors des effets semblables à ceux de l'érable. Si ce type de scénario se réalisait, les castors seraient contraints à de fortes modifications dans leur régime alimentaire, afin de s'adapter à la nouvelle composition forestière. En effet, si les frênes étaient remplacés en grande majorité par des essences non sélectionnées par le castor, c'est probablement là que la perte de qualité de l'habitat serait la plus manifeste pour le castor. Cette diminution de la qualité de l'habitat devrait réduire la taille des groupes de castors, et donc la densité des populations de castors dans les forêts ripariennes. Les castors étant connus pour être moins sélectifs dans les habitats de moindre qualité (Gallant *et al.*, 2004), il est possible d'envisager qu'ils consommeraient les arbres proportionnellement à leur disponibilité si les frênes étaient remplacés majoritairement par des essences généralement non sélectionnées. Les castors seraient alors moins nombreux, n'auraient plus d'espèces préférées à consommer et seraient contraints de consommer des essences non appréciées. Ce changement de comportement alimentaire diminuerait d'autant plus l'effet actuel des castors sur les forêts ripariennes et pourrait, à terme, altérer la dynamique forestière de cet écosystème.

Le remplacement par le genre *Acer* serait également un scénario qui aurait le potentiel de modifier les communautés d'invertébrés du sol. En effet, le troisième chapitre de cette thèse a montré que dans une litière composée de frêne et d'érable, le frêne augmentait clairement sa vitesse de décomposition, ce qui est cohérent avec la littérature sur le sujet (Palik *et al.*, 2005). La vitesse de décomposition de la litière influençait à son tour directement la diversité taxinomique de plusieurs familles d'invertébrés, notamment trois familles de collemboles, qui peuvent jouer des rôles écologiques importants, notamment dans le contrôle des communautés microbiennes et en affectant la dynamique des premiers stades de décomposition de la litière (Potapov *et al.*, 2016). Il est certain qu'un remplacement des frênes par les érables constituerait des changements à long terme dans les communautés d'invertébrés, une perte de biodiversité, et potentiellement une modification des fonctions et services écosystémiques en découlant. À l'inverse, un remplacement par le tilleul d'Amérique (*Tilia americana*) pourrait permettre de réduire l'effet de la disparition du frêne sur les invertébrés du sol, car il semble que sa litière soit très labile, parfois même considérée comme plus labile que celle du frêne (Jacob *et al.*, 2010b; Madritch & Cardinale, 2007; Petersen *et al.*, 1974). Un tel scénario pourrait donc minimiser les impacts pour les familles d'invertébrés qui sont favorisées par une vitesse de décomposition élevée. Cela étant dit, étant donné l'abondance sporadique de ce genre dans les forêts ripariennes dominées par le frêne, il semble peu probable qu'il devienne dominant.

Ultimement, l'impact de la disparition du genre *Fraxinus* sur les forêts ripariennes dépendra en grande partie des essences de remplacements, car de ces dernières dépendra la densité des castors, et la modification potentielle de leur régime alimentaire. L'effet du remplacement du frêne par d'autres essences sur les densités de castors dépendra bien entendu également du bénéfice énergétique que les castors seront en mesure de réaliser sur ces essences, que ce soit par leur apport énergétique, mais également suivant le temps de manipulation nécessaire à leur consommation, et de leur digestibilité (Doucet & Fryxell, 1993). Il ne semble actuellement pas possible de dresser des prévisions plus précises sans savoir comment le remplacement des frênes par d'autres essences se déroulera. Les différents scénarios mentionnés précédemment sont schématisés ci-dessous (figure 4.1), il est cependant à noter que l'hétérogénéité et la diversité des forêts ripariennes impliquent probablement que ces scénarios coexisteront, et pourraient même être plus complexes dépendamment de la succession forestière qui se mettra en place. Sur l'ensemble des scénarios présentés, le remplacement des frênes par l'érable est potentiellement le plus probable, car ce genre peut être considéré comme pionnier, et va également devenir le genre le plus présent avec la disparition du frêne. Le scénario le plus à gauche, qui voit des peuplements de frênes se rétablir, au moins partiellement, est très improbable. Il sert ici davantage de point de référence, afin de mettre en avant le fait que l'ensemble des autres scénarios proposés se traduit par des modifications des communautés d'invertébrés, des modifications de la dynamique des populations de castors, ou des deux.

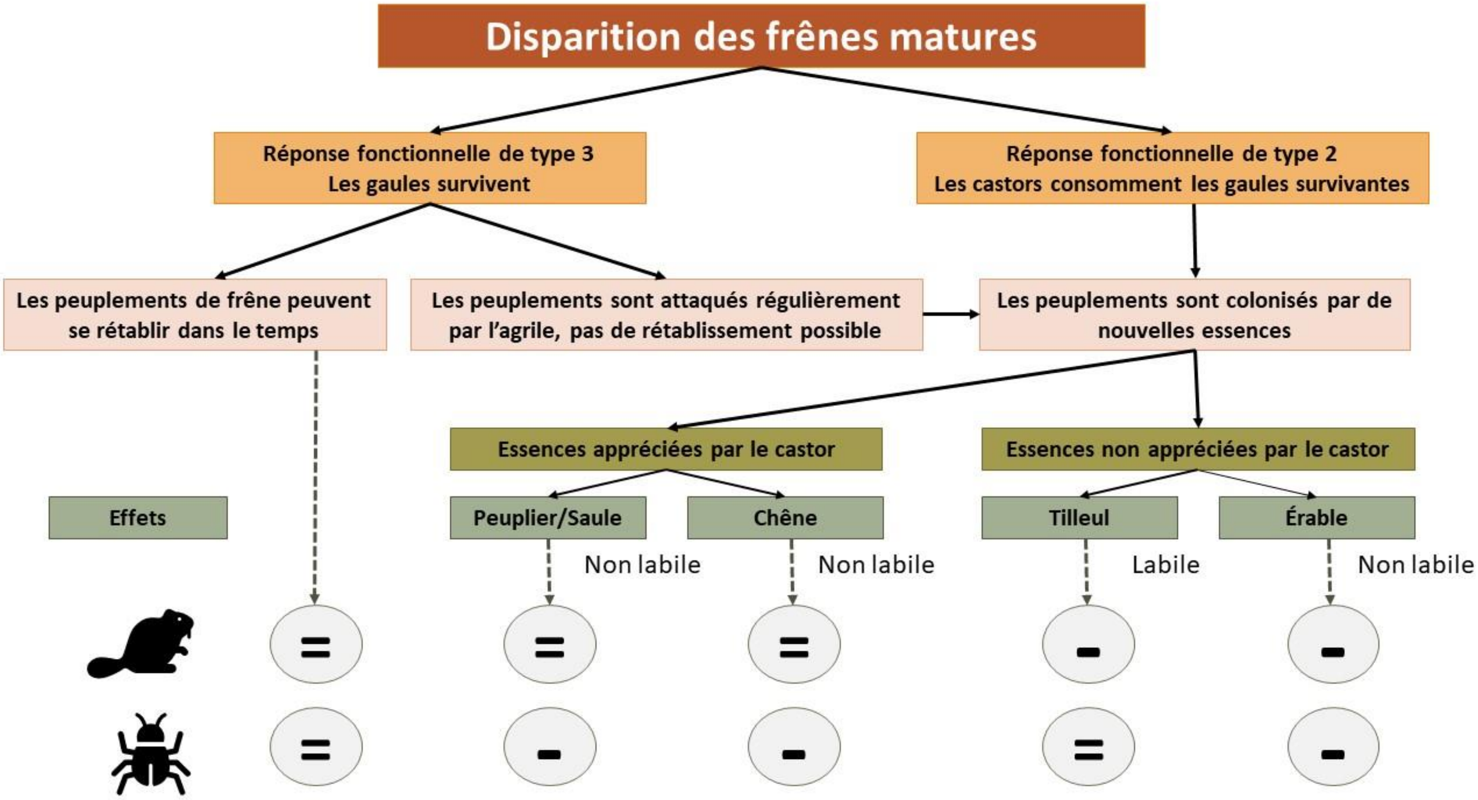

Figure 4.1 Diagramme représentant différents scénarios faisant suite à la mort des arbres de frêne, et les conséquences de ceux-ci sur les castors (régime alimentaire et densités de population) et sur les communautés d'invertébrés.

4.3 Importance de la thèse de doctorat.

Les différents chapitres de cette thèse auront permis l’acquisition de connaissances nouvelles, tant sur le plan fondamental qu’appliqué. Le premier chapitre aura permis de mettre en évidence le rôle majeur du frêne pour l’alimentation du castor dans les forêts ripariennes où celui-ci domine. Bien que cette information ait déjà été suggérée dans certains articles, il était essentiel de le déterminer pour les forêts ripariennes du sud du Québec, car la sélection alimentaire du castor dépend systématiquement des essences retrouvées localement, et qu’aucune étude à ce jour n’avait été réalisée dans des forêts ripariennes aussi diversifiées et avec des essences similaires. Le second chapitre aura permis de montrer que la qualité de l’habitat peut entrainer des modifications de la taille du groupe pour une espèce sociale territoriale, sans pour autant qu’un effet sur la taille du territoire ne soit observé. Ce résultat est sans conteste le plus important de cette thèse sur le point de vue de l’écologie comportementale et des hypothèses l’entourant pour les espèces territoriales. En effet, comme mentionné dans le chapitre 2 et plus haut dans la conclusion, les hypothèses sur la territorialité auraient favorisé une modification de la taille du territoire, ce qui implique que des mécanismes -qui restent encore à être déterminés- peuvent diminuer les coûts liés à la territorialité. Enfin, le troisième chapitre aura permis de mettre en évidence les modifications que la disparition du frêne allait probablement entrainer sur la biodiversité des invertébrés du sol, tant par la modification structurelle de la forêt que par la modification de la litière. L’ensemble de ces trois chapitres permet de mieux concevoir comment les forêts ripariennes vont être modifiées par la disparition du frêne, et permet d’entrevoir des pistes de gestion pour minimiser son effet, et espérer un jour atteindre un certain niveau de résilience, par exemple en favorisant l’hétérogénéité des forêts ripariennes.

4.4 Limites de la thèse de doctorat et perspectives de recherche

4.4.1 Échelle spatiale et temporelle

Une critique certaine qui pourrait être réalisée sur le troisième chapitre de ce doctorat est l’échelle temporelle à laquelle il a été réalisé. En effet, les récoltes d’invertébrés du sol ont été réalisées moins de deux ans après que les parcelles ont été coupées. Ce délai ne laissait pas nécessairement assez de temps pour que les communautés d’invertébrés répondent complètement à la simulation de la perturbation. En effet, le bois mort qui peut être déterminant pour certaines familles d'invertébrés (Grodsky *et al.*, 2018b) n'avait pas eu assez de temps pour commencer à se décomposer. De même, la litière, bien que déjà différente du fait de la coupe, devait probablement encore être en partie composée par les résidus des années précédentes. Par ailleurs, il est connu que certaines communautés d'invertébrés peuvent se modifier pendant plusieurs années à la suite d'une perturbation (Trager *et al.*, 2013). De plus, les parcelles coupées dans le cadre de ce chapitre étaient relativement petites (400 à 800m^2), et sont donc très affectées par des effets de bordures. La disparition de la canopée, ou même de la litière de frênes, pourrait être sous-évaluée dans cette expérience. Cela dit dans notre cas spécifique, l'étude étant réalisée dans un parc national, il était difficile d'obtenir une autorisation pour couper des parcelles plus grandes. Pour toutes ces raisons, les résultats du chapitre 3 sous-estiment probablement l'effet de la disparition des frênes sur les communautés d'invertébrés. Toutefois, le fait que des différences dans les communautés soient observées malgré ces limites inhérentes de notre protocole expérimental suggère que l'invasion de l'agrile aura très clairement des effets importants sur les communautés de ces forêts.

Une des critiques réalisées lors de la revue par les pairs du premier article soumis était l'échelle à laquelle l'étude avait été réalisée. En effet, le parc national de Plaisance est un parc relativement petit (28 km^2), ce qui peut remettre en question la portée de ces résultats. En réalité, les forêts du parc sont très représentatives d'un grand nombre de forêts ripariennes du bassin de l'Outaouais et des plaines du Saint-Laurent. Cette étude n'a pas pour vocation d'être transposable à toutes les forêts ripariennes, mais seulement celles qui sont dominées par le frêne, et dans lesquelles les essences comme le peuplier faux-tremble sont relativement rares, comme c'est le cas dans le domaine bioclimatique étudié.

Pour pallier ces critiques, des inventaires supplémentaires d'invertébrés du sol pourraient par exemple être réalisés dans les mêmes parcelles, à intervalle régulier, afin de suivre l'évolution des communautés d'invertébrés une fois que le bois mort commencera à se décomposer, puis lorsque la canopée se refermera progressivement, afin de déterminer quelles essences d'arbres permettent la résilience des communautés d'invertébrés, et lesquelles ne la permettent pas. Par ailleurs, il serait pertinent de trouver des forêts semblables pour lesquelles la même expérience peut être réalisée, mais avec des parcelles plus grandes, afin de prendre en compte l'effet de bordure, et d'estimer plus précisément l'effet de l'agrile du frêne sur les communautés d'invertébrés du sol.

4.4.2 Réponse partielle

Bien que les résultats obtenus pour chacun des trois chapitres de ce doctorat soient inédits, il est évident qu'ils ne permettent pas à eux seuls de prédire comment seront constituées les forêts ripariennes dominées par le frêne lorsque celui-ci viendra à disparaitre. En effet, les deux premiers chapitres permettent de mieux comprendre la réponse potentielle que pourra avoir le castor face à la disparition du frêne, et donc comment il pourrait façonner les forêts dans le futur, cependant les études proposées ne s'intéressaient qu'aux arbres et arbustes, mais les autres strates composant la forêt n'ont pas été étudiées. L'ouverture brutale de la canopée va pourtant nécessairement entraîner des répercussions sur celles-ci, comme cela a déjà été démontré dans d'autres études (Engelken *et al.*, 2020). De la même façon, le troisième chapitre ne s'intéressait qu'à l'effet de la disparition du frêne sur les communautés d'invertébrés du sol, ce qui est certes une information capitale à connaitre, mais qui ne permet tout de même pas de déterminer entièrement l'importance du frêne pour la biodiversité animale des forêts ripariennes dominées par le frêne. En effet, les invertébrés constituent la base du réseau trophique, et vont être d'une importance capitale pour d'autres taxons vertébrés, comme les micromammifères, les amphibiens, les oiseaux et les poissons (Collier *et al.*, 2002; Murakami & Nakano, 2001; Ramey & Richardson, 2017; Wipfli, 1997). Bien que la disparition du frêne ait déjà été démontrée comme ayant le potentiel d'impacter les taxons vertébrés, comme les amphibiens ou les oiseaux, cette étude ne s'intéressait qu'à la création de grandes trouées dans la canopée qui constituerait une perte de connectivité, et pas aux changements que la nouvelle litière pouvait engendrer (Grinde *et al.*, 2022).

Pour ces raisons, étudier les autres strates de la végétation et les autres taxons d'animaux pourraient être particulièrement intéressants pour répondre plus précisément à la question qui était posée dans ce doctorat. Il pourrait même être envisagé d'étendre cette étude à d'autres règnes, comme les champignons ou les bactéries, qui pourraient être affectés par le changement dans la composition de la litière, et dont les rôles écologiques sont nombreux, comme le transfert des nutriments ou la décomposition de la litière (Haro & Benito, 2019; Helfrich *et al.*, 2015).

4.4.3 Réponse fonctionnelle

Finalement, le fait que nous n'ayons pas été en mesure de déterminer le type de réponse fonctionnelle des castors face aux frênes nous a limités dans notre capacité à déterminer l'avenir des frênes dans les forêts ripariennes. Déterminer cette réponse fonctionnelle aurait permis de mieux comprendre si l'action du castor serait complémentaire à celle de l'agrile du frêne, provoquant ainsi la disparition de toutes les tiges de frêne en forêt riparienne, ou si au contraire, la diminution de la densité des frênes par l'agrile allait provoquer une diminution du taux de consommation par le castor.

Il pourrait donc être très pertinent de réaliser une expérience de type « cafeteria » en milieu contrôlé, c'est-à-dire une expérience dans laquelle le nombre de chacun des items alimentaires, et le temps de manipulation sont contrôlés (Fryxell *et al.*, 1994; Fryxell & Doucet, 1993), afin de pouvoir moduler la densité des frênes et celle des autres genres d'arbres, afin de déterminer la réponse fonctionnelle des castors. Il serait également crucial de déterminer sa réponse fonctionnelle pour toutes les autres essences majoritaires dans ce type de forêt, car cela permettrait de concevoir un modèle prévisionnel vraisemblable de la nouvelle dynamique forestière qui se mettra en place après l'extinction locale des frênes à la suite de l'invasion de l'agrile du frêne dans les forêts ripariennes.

4.5 Conclusion générale

Les trois chapitres présentés ici permettent de confirmer que les frênes jouent un rôle déterminant pour la biodiversité des forêts ripariennes dominées par ces derniers. Cependant, il n'est pas encore possible de déterminer avec précision à quoi ressembleront les forêts ripariennes du futur, et quelle sera la biodiversité qu'elles abriteront. Bien que l'avenir des forêts ripariennes dominées par les frênes soit incertain, il est possible grâce aux résultats de la présente thèse de formuler des recommandations pour minimiser l'impact de la disparition du frêne.

Étant donné qu'aucun genre ne semble avoir le potentiel de remplacer le frêne pour l'ensemble des facettes qui font de lui une essence primordiale pour les forêts ripariennes, il est possible que la clé pour sauvegarder au moins une partie de leur biodiversité soit l'hétérogénéité de ces forêts. En effet, comme cela a pu être suggéré dans cette thèse, certaines essences auraient le potentiel de réduire les modifications de régime alimentaire et de densités des castors, et d'autres auraient le potentiel de réduire les impacts que subiront les communautés d'invertébrés du sol. Bien entendu, il serait tout de même préférable de tester avec une expérience *in-situ* les effets de ces différentes essences sur les communautés animales et végétales, car cette thèse, si tant est qu'elle permette de réaliser de telles suggestions, ne permet pas de le démontrer d'une manière causale.

Enfin, cette thèse a permis de mettre en lumière l'importance écologique des frênes dans les forêts ripariennes tempérées. Le concept d'espèce clé de voûte « *keystone* » (*sensu* Paine, 1969) est vague, et peut avoir de nombreuses définitions (Mills *et al.,* 1993), mais peut être appliqué pour des arbres dont le rôle est primordial pour la survie d'espèces animales, comme cela a déjà été mis en évidence, par exemple pour le peuplier (*P. tremula* L.) dans les forêts boréales (Kivinen *et al.*, 2020). Les frênes, notamment en Europe (*F. excelsior* et *F. angustifolia*), ont déjà été caractérisés d'espèces clé de voûte (George *et al.*, 2022). Le frêne noir, quant à lui, est souvent mentionné comme espèce culturelle clé de voûte, entre autres pour les Premières Nations (Costanza *et al.*, 2017). D'autres études ont déjà laissé penser que le frêne pourrait être un genre clé de voûte dans certains écosystèmes, puisque des dizaines d'espèces d'arthropodes seraient à risque probable d'extinction si ce genre venait à disparaitre (Gandhi & Herms, 2010b). La présente thèse de doctorat constitue un argument de plus pour que le frêne noir et le frêne d'Amérique, les deux espèces de frênes les plus présentes dans les forêts étudiées ici, puissent toutes deux être considérées comme des espèces clé de voûte. Les effets probables de la disparition du frêne qui ont été mis en évidence dans cette thèse semblent être de grandes envergures. D'une part, par la modification des communautés d'invertébrés du sol, qui pourraient elles-mêmes avoir des retombées sur d'autres taxons du réseau trophique (Huryn, 1998), et sur de nombreux services écosystémiques (Lavelle *et al.*, 2006), d'autre part, par la modification probable du régime alimentaire et des densités du castor, une espèce fournissant de nombreux services écosystémiques (Thompson *et al.*, 2021) et qui est considérée comme une espèce ingénieure et donc elle-même clé de voûte (Naiman *et al.*, 1986; Rosell *et al.*, 2005).

Il est nécessaire de poursuivre les recherches pour déterminer plus précisément l'effet qu'aura la disparition du frêne sur les communautés d'invertébrés et les populations de castors, afin de mieux comprendre l’effet que cela aura sur la composition forestière et la biodiversité animale, et ultimement de pouvoir comprendre les effets profonds que cela pourra entrainer sur l’écosystème.

BIBLIOGRAPHIE

Abernethy, B., & Rutherfurd, I. D. (2000). The effect of riparian tree roots on the mass-stability of riverbanks. *Earth Surface Processes and Landforms*, *25*, 921–937.

Ahlgren, I. F., & Ahlgren, C. E. (1960). Ecological effects of forest fires. *The Botanical Review*, *26*(4), 483–533.

Ahn, C., Moser, K. F., Sparks, R. E., & White, D. C. (2007). Developing a dynamic model to predict the recruitment and early survival of black willow (Salix nigra) in response to different hydrologic conditions. *Ecological Modelling*, *204*(3–4), 315–325. https://doi.org/10.1016/j.ecolmodel.2007.01.006

Aleksiuk, M., & Cowan, I. M. (1969). Aspects of seasonal energy expenditure in the beaver (Castor canadensis Kuhl) at the northern limit of its distribution. *Canadian Journal of Zoology* , *47*(4), 471–481. https://doi.org/10.1139/z69-086

Alexander, H. D., & Arthur, M. A. (2014). Increasing Red Maple Leaf Litter Alters Decomposition Rates and Nitrogen Cycling in Historically Oak-Dominated Forests of the Eastern U.S. *Ecosystems*, *17*(8), 1371–1383. https://doi.org/10.1007/s10021-014-9802-4

Aljanabi, S. M., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. In *Nucleic Acids Research* (Vol. 25, Issue 22). Oxford University Press.

Amlin, N. M., & Rood, S. B. (2002). Comparative Tolerances Of Riparian Willows And Cottonwoods To Water-Table Decline. In *Wetlands* (Vol. 22, Issue 2).

Aubin, I., Cardou, F., Ryall, K., Kreutzweiser, D., & Scarr, T. (2015). Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. *The Forestry Chronicle*, *91*(3), 291–298.

Aulen, M., Shipley, B., & Bradley, R. (2012). Prediction of in situ root decomposition rates in an interspecific context from chemical and morphological traits. *Annals of Botany*, *109*(1), 287–297. https://doi.org/10.1093/aob/mcr259

Babl-Plauche, E. K., Alexander, H. D., Siegert, C. M., Willis, J. L., & Berry, A. I. (2022). Mesophication of upland oak forests: Implications of species-specific differences in leaf litter decomposition rates and fuelbed composition. *Forest Ecology and Management*, *512*. https://doi.org/10.1016/j.foreco.2022.120141

Barnes, W. J., & Dibble, E. (1988). The effects of beaver in riverbank forest succession. *Canadian Journal of Botany*, *66*, 40–44. https://doi.org/10.1139/b88-005

Beng, K. C., Tomlinson, K. W., Shen, X. H., Surget-Groba, Y., Hughes, A. C., Corlett, R. T., & Slik, J. W. F. (2016). The utility of DNA metabarcoding for studying the response of arthropod diversity and composition to land-use change in the tropics. *Scientific Reports*, *6*. https://doi.org/10.1038/srep24965

Bergerud, A. T., & Miller, D. R. (1977). Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology*, *55*, 1480–1492. www.nrcresearchpress.com

Bergman, B. G., Bump, J. K., & Romanski, M. C. (2018). Revisiting the role of aquatic plants in beaver habitat selection. *American Midland Naturalist*, *179*(2), 222–246. https://doi.org/10.1674/0003-0031-179.2.222

Beudert, B., Bässler, C., Thorn, S., Noss, R., Schröder, B., Dieffenbach-Fries, H., Foullois, N., & Müller, J. (2015). Bark Beetles Increase Biodiversity While Maintaining Drinking Water Quality. *Conservation Letters*, *8*(4), 272–281. https://doi.org/10.1111/conl.12153

Blaxter, M. L. (2004). The promise of a DNA taxonomy. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 359, Issue 1444, pp. 669–679). Royal Society. https://doi.org/10.1098/rstb.2003.1447

Boulanger, Y., Arseneault, D., Morin, H., Jardon, Y., Bertrand, P., & Dagneau, C. (2012). Dendrochronological reconstruction of spruce budworm (Choristoneura fumiferana) outbreaks in southern Quebec for the last 400 years. *Canadian Journal of Forest Research*, *42*(7), 1264–1276. https://doi.org/10.1139/X2012-069

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *The Wilson Bulletin*, 160–169.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach.* (Springer-Verlag).

Burke, D. J., Weintraub, M. N., Hewins, C. R., & Kalisz, S. (2011). Relationship between soil enzyme activities, nutrient cycling and soil fungal communities in a northern hardwood forest. *Soil Biology and Biochemistry*, *43*(4), 795–803. https://doi.org/10.1016/j.soilbio.2010.12.014

Burst, T. L., & Pelton, M. R. (1983). Black bear mark trees in the smoky mountains. *Bears : Their Biology and Management*, 45–53.

Busher, P. E. (1996). Food Caching Behavior of Beavers (Castor canadensis): Selection and Use of Woody Species. *The American Midland Naturalist*, *135*(2), 343–348. http://www.jstor.orgURL:http://www.jstor.org/stable/2426717

Busher, P. E., Warner, R. J., & Jenkins, S. H. (1983). American Society of Mammalogists Population Density, Colony Composition, and Local Movements in Two Sierra Nevadan Beaver Populations. *Journal of Mammalogy*, *64*(2), 314–318. http://www.jstor.orgURL:http://www.jstor.org/stable/1380566http://www.jstor.org/stable/1380566?seq=1&cid=pdf-reference#references_tab_contents

Buss, D. F., & Vitorino, A. S. (2010). Rapid Bioassessment Protocols using benthic macroinvertebrates in Brazil: Evaluation of taxonomic sufficiency. *Journal of the North American Benthological Society*, *29*(2), 562–571. https://doi.org/10.1899/09-095.1

Calsbeek, R., & Sinervo, B. (2002). An experimental test of the ideal despotic distribution. *Journal of Animal Ecology*, *71*, 513–523. https://doi.org/10.1046/j.1365-2656.2002.00619.x

Campbell, R. D., Rosell, F., Nolet, B. A., & Dijkstra, V. A. A. (2005). Territory and group sizes in Eurasian beavers (Castor fiber): Echoes of settlement and reproduction? *Behavioral Ecology and Sociobiology*, *58*(6), 597–607. https://doi.org/10.1007/s00265-005-0942-6

Černecká, Ľ., Mihál, I., Gajdoš, P., & Jarčuška, B. (2020). The effect of canopy openness of European beech (Fagus sylvatica) forests on ground-dwelling spider communities. *Insect Conservation and Diversity*, *13*(3), 250–261. https://doi.org/10.1111/icad.12380

Champagne, E., Dumont, A., Tremblay, J. P., & Côté, S. D. (2018). Forage diversity, type and abundance influence winter resource selection by white-tailed deer. *Journal of Vegetation Science*, *29*(4), 619–628. https://doi.org/10.1111/jvs.12643

Chauvet, E. (1987). Changes in the chemical composition of alder, poplar and willow leaves during decomposition in a river. In *Hydrobiologia* (Vol. 148).

Collen, P., & Gibson, R. J. (2001). The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish-a review. In *Reviews in Fish Biology and Fisheries* (Vol. 10).

Collier, K. J., Bury, S., & Gibbs, M. (2002). A stable isotope study of linkages between stream and terrestrial food webs through spider predation. *Freshwater Biology*, *47*(9), 1651–1659. https://doi.org/10.1046/j.1365-2427.2002.00903.x

Cook, J. E. (2005). Torrey Botanical Society Vegetation Changes in a Central Wisconsin Floodplain from Pre-Settlement to the Mid-21st Century. *The Journal of the Torrey Botanical Society*, *132*(3), 492–504. http://www.jstor.orgURL:http://www.jstor.org/stable/20063788

Cooper, M. M. D., Patil, S. D., Nisbet, T. R., Thomas, H., Smith, A. R., & McDonald, M. A. (2021). Role of forested land for natural flood management in the UK: A review. In *Wiley*

Interdisciplinary Reviews: Water (Vol. 8, Issue 5). John Wiley and Sons Inc. https://doi.org/10.1002/wat2.1541

Costanza, K. K. L., Livingston, W. H., Kashian, D. M., Slesak, R. A., Tardif, J. C., Dech, J. P., Diamond, A. K., Daigle, J. J., Ranco, D. J., Neptune, J. S., Benedict, L., Fraver, S. R., Reinikainen, M., & Siegert, N. W. (2017). The precarious state of a cultural keystone species: Tribal and biological assessments of the role and future of black ash. In *Journal of Forestry* (Vol. 115, Issue 5, pp. 435–446). Society of American Foresters. https://doi.org/10.5849/jof.2016-034R1

Crandall, R. M., Hayes, C. R., & Ackland, E. N. (2003). Application of the intermediate disturbance hypothesisto flooding. *Community Ecology* , *4*(2), 225–232.

Crawford, J. C., Liu, Z., Nelson, T. A., Nielsen, C. K., & Bloomquist, C. K. (2008). Microsatellite Analysis Of Mating And Kinshipin Beavers (Castor canadensis). *Journal of Mammalogy*, *89*(3), 575–581. https://academic.oup.com/jmammal/article/89/3/575/860979

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A., Murphy, E. J., Österblom, H., Paleczny, M., Piatt, J. F., Roux, J. P., Shannon, L., & Sydeman, W. J. (2011). Global seabird response to forage fish depletion - One-third for the birds. *Science*, *334*(6063), 1703–1706. https://doi.org/10.1126/science.1212928

Davis, J. C., Shannon, J. P., Van Grinsven, M. J., Bolton, N. W., Wagenbrenner, J. W., Kolka, R. K., & Pypker, T. G. (2019). Nitrogen cycling responses to simulated emerald ash borer infestation in Fraxinus nigra-dominated wetlands. *Biogeochemistry*, *145*(3), 275–294. https://doi.org/10.1007/s10533-019-00604-2

de Vries, P. G. (1973). *A General Theory On Line Intersect Sampling With Application To Logging Residue Inventory*.

Deardorff, J. L., & Gorchov, D. L. (2021). Beavers cut, but do not prefer, an invasive shrub, Amur honeysuckle (Lonicera maackii). *Biological Invasions*, *23*(1), 193–204. https://doi.org/10.1007/s10530-020-02365-8

DeStefano, S., Koenen, K. K. G., Henner, C. M., & Strules, J. (2006). Transition to independence by subadult beavers (Castor canadensis) in an unexploited, exponentially growing population. *Journal of Zoology*, *269*(4), 434–441. https://doi.org/10.1111/j.1469-7998.2006.00160.x

Donkor, N. T., & Fryxell, J. M. (2000). Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (Castor canadensis) foraging and edaphic factors. *Plant Ecology*, *148*, 1–12.

Doucet, C. M., & Fryxell, J. M. (1993). The effect of nutritional quality on forage preference by beavers. *Oikos*, 201-208.

Durben, R. M., Walker, F. M., Holeski, L., Keith, A. R., Kovacs, Z., Hurteau, S. R., Lindroth, R. L., Shuster, S. M., & Whitham, T. G. (2021). Beavers, bugs and chemistry: A mammalian herbivore changes chemistry composition and arthropod communities in foundation tree species. *Forests*, *12*(7). https://doi.org/10.3390/f12070877

Edgar, R. C. (n.d.-a). *SINTAX: a simple non-Bayesian taxonomy classifier for 16S and ITS sequences*. https://doi.org/10.1101/074161

Edgar, R. C. (n.d.-b). *UNOISE2: improved error-correction for Illumina 16S and ITS amplicon sequencing*. https://doi.org/10.1101/081257

Engelken, P. J., Benbow, M. E., & McCullough, D. G. (2020). Legacy effects of emerald ash borer on riparian forest vegetation and structure. *Forest Ecology and Management*, *457*. https://doi.org/10.1016/j.foreco.2019.117684

Engelken, P. J., & McCullough, D. G. (2020). Riparian forest conditions along three northern Michigan rivers following emerald ash borer invasion. *Canadian Journal of Forest Research*, *50*(8), 800–810. https://doi.org/10.1139/cjfr-2019-0387

Ewel, K. C., Cressa, C., Kneib, R. T., Lake, P. S., Levin, L. A., Palmer, M. A., Snelgrove, P., & Wall, D. H. (2001). Managing critical transition zones. *Ecosystems*, *4*(5), 452–460. https://doi.org/10.1007/s10021-001-0106-0

Fernandez, A. L., Sheaffer, C. C., Wyse, D. L., Staley, C., Gould, T. J., & Sadowsky, M. J. (2016). Associations between soil bacterial community structure and nutrient cycling functions in long-term organic farm soils following cover crop and organic fertilizer amendment. *Science of the Total Environment*, *566–567*, 949–959. https://doi.org/10.1016/j.scitotenv.2016.05.073

Forio, M. A. E., De Troyer, N., Lock, K., Witing, F., Baert, L., De Saeyer, N., Rîșnoveanu, G., Popescu, C., Burdon, F. J., Kupilas, B., Friberg, N., Boets, P., Volk, M., McKie, B. G., & Goethals, P. (2020). Small patches of riparian woody vegetation enhance biodiversity of invertebrates. *Water (Switzerland)*, *12*(11), 1–21. https://doi.org/10.3390/w12113070

Fretwell, S. D., & Lucas, H. L. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*, 16–35. https://doi.org/10.1007/BF01601953

Fryxell, J. M. (2001). Habitat suitability and source–sink dynamics of beavers. *Journal of Animal Ecology*, *70*, 310–316. https://doi.org/10.1111/j.1365-2656.2001.00492.x

Fryxell, J. M., & Doucet, C. M. (1993). Diet Choice and the Funcional Response of Beavers. *Ecology*, *74*(5), 1297–1306.

Fryxell, J. M., Vamosi, ; S M, Walton, R. A., & Doucet, ; C M. (1994). Retention Time and the Functional Response of Beavers. *Oikos*, *71*(2), 207–214.

Gagnon, E., & Gangbazo, G. (2007). *Efficacité des bandes riveraines : analyse de la documentation scientifique et perspectives*.

Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K., & Standovár, T. (2006). Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology*, *183*(1), 133–145. https://doi.org/10.1007/s11258-005-9012-4

Gallant, D., Bérubé, C. H., Tremblay, E., & Vasseur, L. (2004). An extensive study of the foraging ecology of beavers (Castor canadensis) in relation to habitat quality. *Canadian Journal of Zoology*, *82*(6), 922–933. https://doi.org/10.1139/Z04-067

Gandhi, K. J. K., & Herms, D. A. (2010a). Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions*, *12*(2), 389–405. https://doi.org/10.1007/s10530-009-9627-9

Gandhi, K. J. K., & Herms, D. A. (2010b). North American arthropods at risk due to widespread Fraxinus mortality caused by the alien Emerald ash borer. *Biological Invasions*, *12*(6), 1839–1846. https://doi.org/10.1007/s10530-009-9594-1

Gandhi, K. J. K., Smith, A., Hartzler, D. M., & Herms, D. A. (2014). Indirect effects of emerald ash borer-induced ash mortality and canopy gap formation on epigaeic beetles. *Environmental Entomology*, *43*(3), 546–555. https://doi.org/10.1603/EN13227

Gawlik, D. E. (2002). The effects of prey availability on the numerical response of wading birds. *Ecological Monographs*, *72*(3), 329–346.

George, J. P., Sanders, T. G. M., Timmermann, V., Potočić, N., & Lang, M. (2022). European-wide forest monitoring substantiate the neccessity for a joint conservation strategy to rescue European ash species (Fraxinus spp.). *Scientific Reports*, *12*(1). https://doi.org/10.1038/s41598-022-08825-6

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. https://doi.org/10.1007/s10841-013-9565-9

Gerwing, T. G., Johnson, C. J., & Alström-Rapaport, C. (2013). Factors influencing forage selection by the North American beaver (Castor canadensis). *Mammalian Biology*, *78*(2), 79–86. https://doi.org/10.1016/j.mambio.2012.07.157

Gill, F. B., & Wolf, L. L. (1975). Economics of Feeding Territoriality in the Golden-Winged Sunbird. *Ecology, 56*(2), 333–345. https://doi.org/10.2307/1934964

Graf, P. M., Mayer, M., Zedrosser, A., Hackländer, K., & Rosell, F. (2016). Territory size and age explain movement patterns in the Eurasian beaver. *Mammalian Biology, 81*(6), 587–594. https://doi.org/10.1016/j.mambio.2016.07.046

Grant, J. W. A., Weir, L. K., & Steingrímsson, S. (2017). Territory size decreases minimally with increasing food abundance in stream salmonids: Implications for population regulation. *Journal of Animal Ecology*, *86*(6), 1308–1316. https://doi.org/10.1111/1365-2656.12737

Gregory, S. V, Swanson, F. J., McKee, W. A., & Cummins, K. W. (1991). An Ecosystem Perspective of Riparian Zones. *BioScience*, *41*(8), 540–551. http://www.jstor.org/action/showPublisher?publisherCode=aibs.

Grinde, A. R., Youngquist, M. B., Slesak, R. A., Kolbe, S. R., Bednar, J. D., Palik, B. J., & D’Amato, A. W. (2022). Potential impacts of emerald ash borer and adaptation strategies on wildlife communities in black ash wetlands. *Ecological Applications*. https://doi.org/10.1002/eap.2567

Grodsky, S. M., Moorman, C. E., Fritts, S. R., Campbell, J. W., Sorenson, C. E., Bertone, M. A., Castleberry, S. B., & Wigley, T. B. (2018a). Invertebrate community response to coarse woody debris removal for bioenergy production from intensively managed forests. *Ecological Applications, 28*(1), 135–148. https://doi.org/10.1002/eap.1634

Grodsky, S. M., Moorman, C. E., Fritts, S. R., Campbell, J. W., Sorenson, C. E., Bertone, M. A., Castleberry, S. B., & Wigley, T. B. (2018b). Invertebrate community response to coarse woody debris removal for bioenergy production from intensively managed forests. *Ecological Applications*, *28*(1), 135–148. https://doi.org/10.1002/eap.1634

Gross, H. L. (1991). Dieback and growth loss of sugar maple associated with defoliation by the forest tent caterpillar. *The Forestry Chronicle*, 33–42.

Haack, R. A., Jendek Eduard, Liu Houping, Marchant Kenneth R., Petrice Toby R., Poland Therese M., & Ye Hui. (2002). The Emerald Ash Borer: A New Exotic Pest in North America. *Michigan Entomological Society*, *47*(3 and 4), 1–5.

Hall, J. G. (1960). Willow and aspen in the ecology of beaver on Sagehen Creek, California. *Ecology*, *41*(3), 484–494. https://doi.org/10.2307/1933323

Halofsky, J. E., Peterson, D. L., & Harvey, B. J. (2020). Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. In *Fire Ecology* (Vol. 16, Issue 1). Springer. https://doi.org/10.1186/s42408-019-0062-8

Hammill, E., Petchey, O. L., & Anholt, B. R. (2010). Predator functional response changed by induced defenses in prey. *American Naturalist*, *176*(6), 723–731. https://doi.org/10.1086/657040

Harmon, M. E., & Sexton, J. (1996). *Guidelines for Measurements of Woody Detritus in Forest Guidelines for Measurements of Woody Detritus in Forest Ecosystems Ecosystems*. https://digitalrepository.unm.edu/lter_reports

Haro, R., & Benito, B. (2019). The role of soil fungi in k+ plant nutrition. In *International Journal of Molecular Sciences* (Vol. 20, Issue 13). MDPI AG. https://doi.org/10.3390/ijms20133169

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005a). Biodiversity and litter decomposition in terrestrial ecosystems. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 36, pp. 191–218). https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hättenschwiler, S., Tiunov, A. v., & Scheu, S. (2005b). Biodiversity and litter decomposition in terrestrial ecosystems. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 36, pp. 191–218). https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Helfrich, M., Ludwig, B., Thoms, C., Gleixner, G., & Flessa, H. (2015). The role of soil fungi and bacteria in plant litter decomposition and macroaggregate formation determined using phospholipid fatty acids. *Applied Soil Ecology*, *96*, 261–264. https://doi.org/10.1016/j.apsoil.2015.08.023

Herr, J., & Rosell, F. (2004). Use of space and movement patterns in monogamous adult Eurasian beavers (Castor fiber). *Journal of Zoology*, *262*(3), 257–264. https://doi.org/10.1017/S0952836903004606

Herrera, E. A., Salas, V., Congdon, E. R., Corriale, M. J., & Tang-Martínez, Z. (2011). Capybara social structure and dispersal patterns: Variations on a theme. *Journal of Mammalogy*, *92*(1), 12–20. https://doi.org/10.1644/09-MAMM-S-420.1

Hewlett, R. (2000). Implications of taxonomic resolution and sample habitat for stream classification at a broad geographic scale. In *Am. Benthol. Soc* (Vol. 19, Issue 2).

Hinde, R. A. (1956). The biological significance of the territories of birds. *Ibis*, *93*(3), 340–369.

Hixon, M. A. (1980). Food production and competitor density as the determinants of feeding territory size. *The American Naturalist*, *115*(4), 46. http://www.journals.uchicago.edu/t-and-c

Hohwieler, K., Rosell, F., & Mayer, M. (2018). Scent-marking behavior by subordinate Eurasian beavers. *Ethology*, *124*(8), 591–599. https://doi.org/10.1111/eth.12762

Holling, C. S. (1959). Some Characteristics of Simple Types of Predation and Parasitism. *The Canadian Entomologist*, *41*(7), 385–398.

Hood, G. A., & Bayley, S. E. (2009). A comparison of riparian plant community response to herbivory by beavers (Castor canadensis) and ungulates in Canada’s boreal mixed-wood forest. *Forest Ecology and Management*, *258*(9), 1979–1989. https://doi.org/10.1016/j.foreco.2009.07.052

Hope, E. S., McKenney, D. W., Pedlar, J. H., Lawrence, K., & MacDonald, H. (2021). Canadian efforts to slow the spread of Emerald Ash Borer (Agrilus planipennis Fairmaire) are economically efficient. *Ecological Economics*, *188*, 107126.

Hunter, M. L., Acuña, V., Bauer, D. M., Bell, K. P., Calhoun, A. J. K., Felipe-Lucia, M. R., Fitzsimons, J. A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C. J., Medellin, R. A., Nelson, E. J., & Poschlod, P. (2017). Conserving small natural features with large ecological roles: A synthetic overview. *Biological Conservation*, *211*, 88–95. https://doi.org/10.1016/j.biocon.2016.12.020

Huryn, A. D. (1998). Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, *115*, 173–183.

Huxley, J. S. (1934). A natural experiment on the territorial instinct. *British Birds*, *27*(10), 270–277.

Ireland, K. B., Moore, M. M., Fulé, P. Z., Zegler, T. J., & Keane, R. E. (2014). Slow lifelong growth predisposes Populus tremuloides trees to mortality. *Oecologia*, *175*(3), 847–859. https://doi.org/10.1007/s00442-014-2951-5

Jacob, M., Viedenz, K., Polle, A., & Thomas, F. M. (2010a). Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (Fagus sylvatica). *Oecologia*, *164*(4), 1083–1094. https://doi.org/10.1007/s00442-010-1699-9

Jacob, M., Viedenz, K., Polle, A., & Thomas, F. M. (2010b). Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (Fagus sylvatica). *Oecologia*, *164*(4), 1083–1094. https://doi.org/10.1007/s00442-010-1699-9

Jacobs, J. (1974). Quantitative Measurement of Food Selection A Modification of the Forage Ratio and Ivlev's Electivity Index. *Oecologia*, *14*, 413–417.

Ji, Y., Ashton, L., Pedley, S. M., Edwards, D. P., Tang, Y., Nakamura, A., Kitching, R., Dolman, P. M., Woodcock, P., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., Hamer, K. C., Wilcove, D. S., Bruce, C., Wang, X., Levi, T., Lott, M., … Yu, D. W. (2013). Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. *Ecology Letters*, *16*(10), 1245–1257. https://doi.org/10.1111/ele.12162

Johnson, C. J. (2013). Identifying ecological thresholds for regulating human activity: Effective conservation or wishful thinking? *Biological Conservation*, *168*, 57–65. https://doi.org/10.1016/j.biocon.2013.09.012

Johnson, D., Kays, R., Blackwell, Paul G, & Macdonald, D. W. (2002). Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution*, *17*(2), 563–570. https://doi.org/10.1016/S0169-5347(02)02619-8

Johnson, M. D. (2007). Measuring Habitat Quality: A Review. *The Condor*, *109*(3), 489–504. https://doi.org/10.1093/condor/109.3.489

Johnston, C. A., & Naiman, R. J. (1990). Browse selection by beaver: effects on riparian forest composition. *Canadian Journal of Forest Research*, *20*, 1036–1043. https://doi.org/10.1139/x90-138

Johnstone, J. F., Chapin, F. S., Hollingsworth, T. N., Mack, M. C., Romanovsky, V., & Turetsky, M. (2010). Fire, climate change, and forest resilience in interior alaska. *Canadian Journal of Forest Research*, *40*(7), 1302–1312. https://doi.org/10.1139/X10-061

Jonczak, J. (2009). Leaf litter fall decomposition in age-differentiated stands of poplar clone Hybrid 275. *Polish Journal of Soil Science*, *42*(2), 159–166. https://www.researchgate.net/publication/273945069

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P., & Lepage, M. (2006). Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. In *Applied Soil Ecology* (Vol. 32, Issue 2, pp. 153–164). https://doi.org/10.1016/j.apsoil.2005.07.004

Karnosky, D. F. (1979). Dutch Elm Disease: A Review of the History, Environmental Implications, Control, and Research Needs. *Environmental Conservation*, *6*(4), 311–322.

Kashian, D. M., & Witter, J. A. (2011). Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management*, *261*(3), 480–488. https://doi.org/10.1016/j.foreco.2010.10.033

Kelemen, K., Mihók, B., Gálhidy, L., & Standovár, T. (2012). Dynamic response of herbaceous vegetation to gap opening in a central European beech stand. *Silva Fennica*, *46*(1), 53–65. https://doi.org/10.14214/sf.65

Kelly, L. T., Brotons, L., & McCarthy, M. A. (2017). Putting pyrodiversity to work for animal conservation. *Conservation Biology*, *31*(4), 952–955. https://doi.org/10.1111/cobi.12861

Kimball, B. A., & Perry, K. R. (2008). Manipulating beaver (Castor canadensis) feeding responses to invasive tamarisk (Tamarix spp.). *Journal of Chemical Ecology*, *34*(8), 1050–1056. https://doi.org/10.1007/s10886-008-9496-1

King, S. L., & Antrobus, T. J. (2005). Relationships between gap makers and gap fillers in an Arkansas floodplain forest. *Journal of Vegetation Science, 16*, 471–480.

Kittle, A. M., Anderson, M., Avgar, T., Baker, J. A., Brown, G. S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B. R., Reid, D. E. B., Rodgers, A. R., Shuter, J., Street, G. M., Thompson, I. D., Vander Vennen, L. M., & Fryxell, J. M. (2015). Wolves adapt territory size, not pack size to local habitat quality. *Journal of Animal Ecology*, *84*(5), 1177–1186. https://doi.org/10.1111/1365-2656.12366

Kivinen, S., Koivisto, E., Keski-Saari, S., Poikolainen, L., Tanhuanpää, T., Kuzmin, A., Viinikka, A., Heikkinen, R. K., Pykälä, J., Virkkala, R., Vihervaara, P., & Kumpula, T. (2020). A keystone species, European aspen (Populus tremula L.), in boreal forests: Ecological role, knowledge needs and mapping using remote sensing. In *Forest Ecology and Management* (Vol. 462). Elsevier B.V. https://doi.org/10.1016/j.foreco.2020.118008

Klooster, W. S., Herms, D. A., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., Gandhi, K. J. K., & Cardina, J. (2014). Ash (Fraxinus spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (Agrilus planipennis). *Biological Invasions*, *16*(4), 859–873. https://doi.org/10.1007/s10530-013-0543-7

Knight, K. S., Brown, J. P., & Long, R. P. (2013). Factors affecting the survival of ash (Fraxinus spp.) trees infested by emerald ash borer (Agrilus planipennis). *Biological Invasions*, *15*(2), 371–383. https://doi.org/10.1007/s10530-012-0292-z

Koivula, M., Punttila, P., Haila, Y., & Nicnielii Koivula Punltila P-, J. M. (1999). *Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest*.

Kolka, R. K., D’Amato, A. W., Wagenbrenner, J. W., Slesak, R. A., Pypker, T. G., Youngquist, M. B., Grinde, A. R., & Palik, B. J. (2018). Review of ecosystem level impacts of emerald ash borer on black ashwetlands: What does the future hold? *Forests*, *9*(4). https://doi.org/10.3390/f9040179

Krebs, P., Pezzatti, G. B., Mazzoleni, S., Talbot, L. M., & Conedera, M. (2010). Fire regime: History and definition of a key concept in disturbance ecology. *Theory in Biosciences*, *129*(1), 53–69. https://doi.org/10.1007/s12064-010-0082-z

Kreutzweiser, D., Dutkiewicz, D., Capell, S., Sibley, P., & Scarr, T. (2020). Changes in streamside riparian forest canopy and leaf litter nutrient flux to soils during an emerald ash borer infestation in an agricultural landscape. *Biological Invasions*, *22*(6), 1865–1878. https://doi.org/10.1007/s10530-020-02223-7

Kreutzweiser, D., Nisbet, D., Sibley, P., & Scarr, T. (2019). Loss of ash trees in riparian forests from emerald ash borer infestations has implications for aquatic invertebrate leaf-litter consumers. *Canadian Journal of Forest Research*, *49*(2), 134–144. https://doi.org/10.1139/cjfr-2018-0283

Kruuk, H., & Parish, T. (1982). Factors affecting population density-, group size and territory size of the European badger, Meles meles. *Journal of Zoology*, *196*, 31–39. https://doi.org/10.1111/j.1469-7998.1982.tb03492.x

Lafond, R., Leblanc, Y., Pilon, C., & Société de la faune et des parcs du Québec. Direction du développement de la faune. (2003). *Bilan du plan d'inventaire aérien des colonies de castors au Québec (1989-1994)*. Société de la faune et des parcs du Québec, Direction du développement de la faune.

Laird-Hopkins, B. C., Bréchet, L. M., Trujillo, B. C., & Sayer, E. J. (2017). Tree functional diversity affects litter decomposition and arthropod community composition in a tropical forest. *Biotropica*, *49*(6), 903–911. https://doi.org/10.1111/btp.12477

Lambeets, K., Vandegehuchte, M. L., Maelfait, J. P., & Bonte, D. (2008). Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*, *77*(6), 1162–1174. https://doi.org/10.1111/j.1365-2656.2008.01443.x

Lasota, J., Piaszczyk, W., & Błońska, E. (2022). Fine woody debris as a biogen reservoir in forest ecosystems. In *Acta Oecologica* (Vol. 115). Elsevier B.V. https://doi.org/10.1016/j.actao.2022.103822

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, *42*(SUPPL. 1). https://doi.org/10.1016/j.ejsobi.2006.10.002

Lecerf, A., & Chauvet, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology*, *9*(5), 598–605. https://doi.org/10.1016/j.baae.2007.11.003

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Leroy, C. J., Whitham, T. G., Wooley, S. C., & Marks, J. C. (2007). Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. In *Am. Benthol. Soc* (Vol. 26, Issue 3).

Li, X., Qu, Z., Zhang, Y., Ge, Y., & Sun, H. (2022). Soil Fungal Community and Potential Function in Different Forest Ecosystems. In *Diversity* (Vol. 14, Issue 7). MDPI. https://doi.org/10.3390/d14070520

Lindeman, A. A., Grant, J. W. A., & Desjardins, C. M. (2015). Density-dependent territory size and individual growth rate in juvenile Atlantic salmon (Salmo salar). *Ecology of Freshwater Fish*, *24*(1), 15–22. https://doi.org/10.1111/eff.12120

Lowrance, R. (2000). *Riparian Forest Ecosystems as Filters for Nonpoint-Source Pollution*.

Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature*, *301*, 379–384. https://doi.org/10.1038/301379a0

MacFarlane, D. W., & Meyer, S. P. (2005). Characteristics and distribution of potential ash tree hosts for emerald ash borer. *Forest Ecology and Management*, *213*, 15–24. https://doi.org/10.1016/j.foreco.2005.03.013

Madritch, M. D., & Cardinale, B. J. (2007). Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: A multi-site experiment along a latitudinal gradient. *Plant and Soil*, *292*(1–2), 147–159. https://doi.org/10.1007/s11104-007-9209-5

Maher, C. R., & Lott, D. F. (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour*, *49*, 1581–1597.

Maisonneuve, C., & Rioux, S. (2001). Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Québec. *Ecosystems and Environment*, *83*, 165–175.

Major, M., Gosselin, Jocelyn., Landry, Yves., Québec (Province). Direction des inventaires forestiers., & Québec (Province). Ministère des ressources naturelles et de la faune. Direction des communications. (2012). *Guide de reconnaissance des types écologiques. Région écologique 1a : plaine du bas Outaouais et de l'archipel de Montréal*. Ministère des ressources naturelles et de la faune, Forêt Québec, Direction des inventaires forestiers.

Marks, C. O. (2017). *The Ecological Role Of American Elm (Ulmus americana L.) In Floodplain Forests Of Northeastern North America*.

Marler, C. A., & Moore, M. C. (1988). Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral Ecology Sociobiology*, *23*, 21–26.

Marshall, J. C., Steward, A. L., & Harch, B. D. (2006). Taxonomic resolution and quantification of freshwater macroinvertebrate samples from an Australian dryland river: The benefits and costs of using species abundance data. *Hydrobiologia*, *572*(1), 171–194. https://doi.org/10.1007/s10750-005-9007-0

Martell, K. A., Foote, A. L., & Cumming, S. G. (2006). Riparian disturbance due to beavers (Castor canadensis) in Alberta's boreal mixedwood forests: Implications for forest management. *Ecoscience*, *13*(2), 164–171. https://doi.org/10.2980/i1195-6860-13-2-164.1

Matthes, J. H., Lang, A. K., Jevon, F. V., & Russell, S. J. (2018). Tree stress and mortality from emerald ash borer does not systematically alter short-term soil carbon flux in a mixed northeastern U.S. forest. *Forests*, *9*(1). https://doi.org/10.3390/f9010037

Mayer, M., Aparicio Estalella, C., Windels, S. K., & Rosell, F. N. (2020). Landscape structure and population density affect intraspecific aggression in beavers. *Ecology and Evolution*, *10*(24), 13883–13894. https://doi.org/10.1002/ece3.6980

Mayer, M., Frank, S. C., Zedrosser, A., & Rosell, F. (2020). Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. *Journal of Animal Ecology*, *89*(2), 577–588. https://doi.org/10.1111/1365-2656.13100

Mayer, M., Zedrosser, A., & Rosell, F. (2017a). Couch potatoes do better: Delayed dispersal and territory size affect the duration of territory occupancy in a monogamous mammal. *Ecology and Evolution*, *7*(12), 4347–4356. https://doi.org/10.1002/ece3.2988

Mayer, M., Zedrosser, A., & Rosell, F. (2017b). When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Animal Behaviour*, *123*, 375–382. https://doi.org/10.1016/j.anbehav.2016.11.020

Milligan, H. E., & Humphries, M. M. (2010). The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. *Oikos*, *119*(12), 1877–1886. https://doi.org/10.1111/j.1600-0706.2010.18160.x

Mills, S. L., Soulé, M. E., & Doak, D. F. (1993). The Keystone-Species Concept in Ecology and Conservation. *BioScience*, *43*(4), 219–224.

Mitchell, S. J. (2013). Wind as a natural disturbance agent in forests: A synthesis. In *Forestry* (Vol. 86, Issue 2, pp. 147–157). https://doi.org/10.1093/forestry/cps058

Mogi, M. (2007). Insects and other invertebrate predators. In *Journal of the American Mosquito Control Association* (Vol. 23, Issue 2 SUPPL., pp. 93–109). American Mosquito Control Association. https://doi.org/10.2987/8756-971x(2007)23[93:iaoip]2.0.co;2

Mosser, A., Fryxell, J. M., Eberly, L., & Packer, C. (2009). Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, *12*(10), 1050–1060. https://doi.org/10.1111/j.1461-0248.2009.01359.x

Moulinier, J., Lorenzetti, F., & Bergeron, Y. (2011). Gap dynamics in aspen stands of the clay belt of northwestern Quebec following a forest tent caterpillar outbreak. *Canadian Journal of Forest Research*, *41*(8), 1606–1617. https://doi.org/10.1139/x11-075

Müller-Schwarze, D. (2011). *The Beaver: Natural history of a wetlands engineer.* (2nd edition). Comstock Publishing Associates.

Müller-Schwarze, D., & Heckman, S. (1980a). The Social Role of Scent Marking in Beaver (Castor canadensis). *Journal of Chemical Ecology*, *6*(1).

Müller-Schwarze, D., & Heckman, S. (1980b). The social role of scent marking in beaver (Castor canadensis). *Journal of Chemical Ecology*, *6*(1), 81–95. https://doi.org/10.1007/BF00987529

Müller-Schwarze, D., Schulte, B. A., Sun, L., Müller-Schwarze, A., & Müller-Schwarze, , Christine. (1994). Red Maple (Acer Rubrum) Inhibits Feeding By Beaver (Castor canadensis). *Journal of Chemical Ecology*, *20*(8).

Murakami, M., & Nakano, S. (2001). Species-specific foraging behavior of birds in a riparian forest. *Ecological Research*, *16*, 913–923.

Musolin, D. L., Selikhovkin, A. V., Peregudova, E. Y., Popovichev, B. G., Mandelshtam, M. Y., Baranchikov, Y. N., & Vasaitis, R. (2021). North-westward expansion of the invasive range of emerald ash borer, agrilus planipennis fairmaire (Coleoptera: Buprestidae) towards the EU: From Moscow to Saint Petersburg. *Forests*, *12*(4), 502. https://doi.org/10.3390/f12040502

Naiman, R. J., & Decamps, H. (1997). The Ecology Of Interfaces-Riparian Zones. *Annual Review of Ecology and Systematics*, 621–658.

Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American Streams by Beaver. *BioScience*, *38*(11), 753–762. http://www.jstor.orgURL:http://www.jstor.org/stable/1310784Accessed:18/06/200814:47

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor Canadensis). *Ecology*, *67*(5), 1254–1269.

Nisbet, D., Kreutzweiser, D., Sibley, P., & Scarr, T. (2015). Ecological risks posed by emerald ash borer to riparian forest habitats: A review and problem formulation with management implications. *Forest Ecology and Management*, *358*, 165–173. https://doi.org/10.1016/j.foreco.2015.08.030

Noble, G. K. (1939). The Role of Dominance in the Social Life of Birds. *The Auk*, *56*(3), 263–273.

Nolet, B. A., & Rosell, F. (1994). Territoriality and time budgets in beavers during sequential settlement. *Canadian Journal of Zoology*, *72*(7), 1227–1237. https://doi.org/10.1139/z94-164

Nummi, P., Liao, W., Huet, O., Scarpulla, E., & Sundell, J. (2019). The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Global Ecology and Conservation*, *20*. https://doi.org/10.1016/j.gecco.2019.e00701

O’Brien, P. A., Tan, S., Yang, C., Frade, P. R., Andreakis, N., Smith, H. A., Miller, D. J., Webster, N. S., Zhang, G., & Bourne, D. G. (2020). Diverse coral reef invertebrates exhibit patterns of phylosymbiosis. *ISME Journal*, *14*(9), 2211–2222. https://doi.org/10.1038/s41396-020-0671-x

Olson, J. S. (1963). Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. *Ecology*, *44*(2), 322–331.

O’Rourke, D. R., Bokulich, N. A., Jusino, M. A., MacManes, M. D., & Foster, J. T. (2020). A total crapshoot? Evaluating bioinformatic decisions in animal diet metabarcoding analyses. *Ecology and Evolution*, *10*(18), 9721–9739. https://doi.org/10.1002/ece3.6594

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, *103*(929), 91-93.

Paine, L. K., & Ribic, C. A. (2002). Comparison of riparian plant communities under four land management systems in southwestern Wisconsin. *Ecosystems and Environment*, *92*, 93–105.

Palik, B., Batzer, D. P., & Kern, C. (2005). Upland Forest Linkages to Seasonal Wetlands: Litter lux, Processing, and Food Quality. *Ecosystems*, *8*, 1–11. https://doi.org/10.10071~1002

Partsch, S., Milcu, A., & Scheu, S. (2006). Decomposers (Lumbricidae, Collembola) affect plant performance in model grasslands of different diversity. *Ecology*, *87*(10), 2548–2558. https://doi.org/10.1890/0012-9658(2006)87[2548:DLCAPP]2.0.CO;2

Patterson, B. R., & Messier, F. O. (2001). Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. *Journal of Mammalogy*, *82*(2), 463–477. https://doi.org/10.1644/1545-1542(2001)082<0463:SOASUO>2.0.CO;2

Payne, N. F. (1982). Colony size, age, and sex structure of Newfoundland beaver. *The Journal of Wildlife Management*, *46*(3), 655–661. https://doi.org/10.2307/3808556

Peres, C. A. (1989). Behavioral Ecology and Sociobiology Costs and benefits of territorial defense in wild golden lion tamarins, Leontopithecus rosMia. *Behavioral Ecology and Sociobiology*, *25*, 227–233.

Perry, K. I., & Herms, D. A. (2016a). Response of the forest floor invertebrate community to canopy gap formation caused by early stages of emerald ash borer-induced ash mortality. *Forest Ecology and Management*, *375*, 259–267. https://doi.org/10.1016/j.foreco.2016.05.034

Perry, K. I., & Herms, D. A. (2016b). Response of the forest floor invertebrate community to canopy gap formation caused by early stages of emerald ash borer-induced ash mortality.

Forest Ecology and Management, *375*, 259–267. https://doi.org/10.1016/j.foreco.2016.05.034

Perry, K. I., Herms, D. A., Klooster, W. S., Smith, A., Hartzler, D. M., Coyle, D. R., & Gandhi, K. J. K. (2018). Downed coarse woody debris dynamics in ash (Fraxinus spp.) stands invaded by emerald ash borer (Agrilus planipennis Fairmaire). *Forests, 9*(4). https://doi.org/10.3390/f9040191

Perry, K. I., Wallin, K. F., Wenzel, J. W., & Herms, D. A. (2018). Forest disturbance and arthropods: Small-scale canopy gaps drive invertebrate community structure and composition. *Ecosphere*, *9*(10). https://doi.org/10.1002/ecs2.2463

Petersen, R. C., Cummins, K. W., & Kellogg, W. K. (1974). Leaf processing in a woodland stream'. In *Freshwat. Biol* (Vol. 4).

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, *307*, 321–326.

Poland, T. M., Chen, Y., Koch, J., & Pureswaran, D. (2015). Review of the emerald ash borer (Coleoptera: Buprestidae), life history, mating behaviours, host plant selection, and host resistance. *Canadian Entomologist*, *147*, 252–262. https://doi.org/10.4039/tce.2015.4

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). TOWARD AN INTEGRATION OF LANDSCAPE AND FOOD WEB ECOLOGY: The Dynamics of Spatially Subsidized Food Webs. *Annual Review of Ecology and Systematics*, *28*, 289–316.

Pollierer, M. M., Langel, R., Körner, C., Maraun, M., & Scheu, S. (2007). The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters*, *10*(8), 729–736. https://doi.org/10.1111/j.1461-0248.2007.01064.x

Potapov, A. A., Semenina, E. E., Korotkevich, A. Y., Kuznetsova, N. A., & Tiunov, A. V. (2016). Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms. *Soil Biology and Biochemistry*, *101*, 20–31. https://doi.org/10.1016/j.soilbio.2016.07.002

Praw, J. C., & Grant, J. W. A. (1999). Optimal Territory Size in the Convict Cichlid. *Behaviour*, *136*(10), 1347–1363.

Przepióra, F., Loch, J., & Ciach, M. (2020). Bark beetle infestation spots as biodiversity hotspots: Canopy gaps resulting from insect outbreaks enhance the species richness, diversity and abundance of birds breeding in coniferous forests. *Forest Ecology and Management*, *473*. https://doi.org/10.1016/j.foreco.2020.118280

Raffel, T. R., Smith, N., Cortright, C., & Gatz, A. J. (2009). Central Place Foraging by Beavers (Castor canadensis) in a Complex Lake Habitat. *The American Midland Naturalist*, *162*(1), 62–73. http://www.jstor.orgURL:http://www.jstor.org/stable/25602298http://www.jstor.org/stable/25602298?seq=1&cid=pdf-reference#references_tab_contents

Ramey, T. L., & Richardson, J. S. (2017). Terrestrial Invertebrates in the Riparian Zone: Mechanisms Underlying Their Unique Diversity. In *BioScience* (Vol. 67, Issue 9, pp. 808–819). Oxford University Press. https://doi.org/10.1093/biosci/bix078

Rand, T. A. (2003). Herbivore-Mediated Apparent Competition Between Two salt Marsh Forbs. *Ecology*, *84*(6), 1517–1526.

Revilla, E., & Palomares, F. (2002). Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, Meles meles. *Journal of Animal Ecology*, *71*(3), 497–512. https://doi.org/10.1046/j.1365-2656.2002.00617.x

Ricotta, C., & Podani, J. (2017). On some properties of the Bray-Curtis dissimilarity and their ecological meaning. *Ecological Complexity*, *31*, 201-205.

Robertson, A., Palphramand, K. L., Carter, S. P., & Delahay, R. J. (2015). Group size correlates with territory size in European badgers: Implications for the resource dispersion hypothesis? *Oikos*, *124*(4), 507–514. https://doi.org/10.1111/oik.01459

Robeson, M. S., O'Rourke, D. R., Kaehler, B. D., Ziemski, M., Dillon, M. R., Foster, J. T., & Bokulich, N. A. (2021). RESCRIPt: Reproducible sequence taxonomy reference database management for the 1 masses. *PLoS Computational Biology*, *17*(11). https://doi.org/10.1101/2020.10.05.326504

Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, *2016*(10). https://doi.org/10.7717/peerj.2584

Rosell, F., & Bjørkøyli, T. (2002). A test of the dear enemy phenomenon in the Eurasian beaver. *Animal Behaviour*, *63*(6), 1073–1078. https://doi.org/10.1006/anbe.2002.3010

Rosell, F., Bozsér, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. *Mammal Rev*, *35*(4), 248–276.

Rosell, F., & Nolet, B. A. (1997). Factors Affecting Scent-Marking Behavior in Eurasian Beaver (Castor fiber). *Journal of Chemical Ecology*, *23*(3).

Rosell, F., & Thomsen, L. R. (2006). Sexual dimorphism in territorial scent marking by adult Eurasian beavers (Castor fiber). *Journal of Chemical Ecology*, *32*(6), 1301–1315. https://doi.org/10.1007/s10886-006-9087-y

Rosner, S., Dupuch, A., & Lorenzetti, F. (2022). Stuck between the mandibles of an insect and of a rodent: where does the fate of ash-dominated riparian temperate forests lie? *Forests*, *13*(11), 1760. https://doi.org/10.3390/f13111760

Rossell, C. R., Arico, S., Clarke, H. D., Horton, J. L., Ward, J. R., & Patch, S. C. (2014). Forage selection of native and nonnative woody plants by Beaver in a rare-shrub community in the

Appalachian Mountains of North Carolina. *Southeastern Naturalist*, *13*(4), 649–662. https://doi.org/10.1656/058.013.0415

Rousseau, J. (1962). Les forêts ripariennes du Québec. *Cahiers de Géographie Du Québec*, *6*(12), 167–182. https://doi.org/10.7202/020379ar

Royama, T. (1984). Population Dynamics of the Spruce Budworm Choristoneura fumiferana. *Ecological Monographs*, *54*(4), 429–462. http://www.jstor.orgURL:http://www.jstor.org/stable/1942595

Rusek, J. (1998). Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation*, *7*, 1207–1219. https://doi.org/10.1023/A:1008887817883

Sarnelle, O., & Wilson, A. E. (2008). Type III functional response in daphnia. *Ecology*, *89*(6), 1723–1732. https://doi.org/10.1890/07-0935.1

Sayer, E. J., Sutcliffe, L. M. E., Ross, R. I. C., & Tanner, E. V. J. (2010). Arthropod abundance and diversity in a lowland tropical forest floor in Panama: The role of habitat space vs. nutrient concentrations. *Biotropica*, *42*(2), 194–200. https://doi.org/10.1111/j.1744-7429.2009.00576.x

Schindler, M. H., & Gessner, M. O. (2009). Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology*, *90*(6), 1641–1649. https://doi.org/10.1890/08-1597.1

Schoener, T. W. (1983). Simple models of optimal feeding-territory size : a reconciliation. *American Naturalist*, *121*(5), 608–629. http://www.journals.uchicago.edu/t-and-c

Sharma, D. K., Tomar, S., & Chakraborty, D. (2017). Role of earthworm in improving soil structure and functioning. *Current Science*, *113*(6).

Sibley, P. K., Dutkiewicz, D., Kreutzweiser, D. P., & Hazlett, P. (2020). Soil and nutrient cycling responses in riparian forests to the loss of Ash (Fraxinus spp. L) from Emerald Ash Borer (Agrilus planipennis, Fairmaire). *Forests, 11*(5). https://doi.org/10.3390/F11050489

Siegert, N. W., Mccullough, D. G., Liebhold, A. M., & Telewski, F. W. (2014). Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. *Diversity and Distributions, 20*(7), 847–858. https://doi.org/10.1111/ddi.12212

Sikes, R. S. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. In *Journal of Mammalogy* (Vol. 97, Issue 3, pp. 663–688). Allen Press Inc. https://doi.org/10.1093/jmammal/gyw078

Siracusa, E., Morandini, M., Boutin, S., Humphries, M. M., Dantzer, B., McAdam, A. G., & Siracusa, E. (2017). Red squirrel territorial vocalizations deter intrusions by conspecific rivals. *Behaviour, 154*(13–15), 1259–1273. https://doi.org/10.1101/448894

Smith, D. W. (1997). *Dispersal strategies and cooperative breeding in beavers*. University of Nevada.

Smith, D. W., & Tyers, D. B. (2012). The history and current status and distribution of beavers in Yellowstone National Park. *Northwest Science*, *86*(4), 276–288. https://doi.org/10.3955/046.086.0404

Smith, J. D., & Goyer, R. A. (1986). Population Fluctuations and Causes of Mortality for the Forest Tent Caterpillar, Malacosoma disstria (Lepidoptera: Lasiocampidae), on Three Different Sites in Southern Louisiana. In *Environ. Entomol* (Vol. 15). http://ee.oxfordjournals.org/

Spence, C. E., & Maclean, D. A. (2011). Comparing growth and mortality of a sprucebudworm (Choristoneura fumiferana) inspired harvest versus a spruce budworm outbreak. *Canadian Journal of Forest Research*, *41*(11), 2176–2192. https://doi.org/10.1139/x11-129

Stehle, C. M., Battles, A. C., Sparks, M. N., & Johnson, M. A. (2017). Prey availability affects territory size, but not territorial display behavior, in green anole lizards. *Acta Oecologica*, *84*, 41–47. https://doi.org/10.1016/j.actao.2017.08.008

Steyaert, M., Priestley, V., Osborne, O., Herraiz, A., Arnold, R., & Savolainen, V. (2020). Advances in metabarcoding techniques bring us closer to reliable monitoring of the marine benthos. *Journal of Applied Ecology*, *57*(11), 2234–2245. https://doi.org/10.1111/1365-2664.13729

Stoffyn-Egli, P., & Willison, J. H. M. (2011). Including wildlife habitat in the definition of riparian areas: The beaver (Castor canadensis) as an umbrella species for riparian obligate animals. In *Environmental Reviews* (Vol. 19, Issue 1, pp. 479–493). National Research Council of Canada. https://doi.org/10.1139/a11-019

Sun, L., Müller-Schwarze, D., & Schulte, B. A. (2000). Dispersal pattern and effective population size of the beaver. *Canadian Journal of Zoology*, *78*(3), 393–398. https://doi.org/10.1139/z99-226

Swan, C. M., & Palmer, M. A. (2006). Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. *Oecologia*, *147*(3), 469–478. https://doi.org/10.1007/s00442-005-0297-8

Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews of the Cambridge Philosophical Society*, *91*(3), 760–781. https://doi.org/10.1111/brv.12193

Thompson, S., Vehkaoja, M., Pellikka, J., & Nummi, P. (2021). Ecosystem services provided by beavers Castor spp. In *Mammal Review* (Vol. 51, Issue 1, pp. 25–39). Blackwell Publishing Ltd. https://doi.org/10.1111/mam.12220

Trager, M. D., Ristau, T. E., Stoleson, S. H., Davidson, R. L., & Acciavatti, R. E. (2013). Carabid beetle responses to herbicide application, shelterwood seed cut and insect defoliator outbreaks.

Forest Ecology and Management, *289*, 269–277. https://doi.org/10.1016/j.foreco.2012.10.025

Tumulty, J. P. (2018). Dear enemy effect. In *Encyclopedia of animal cognition and behavior* (pp. 1–4). Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_693-1

Turnbull, M. S., & Stebaeva, S. (2019). Collembola of Canada. *ZooKeys*, *819*, 187–195. https://doi.org/10.3897/zookeys.819.23653

Ulyshen, M. D. (2016). Wood decomposition as influenced by invertebrates. *Biological Reviews*, *91*(1), 70–85. https://doi.org/10.1111/brv.12158

Ulyshen, M. D., Klooster, W. S., Barrington, W. T., & Herms, D. A. (2011). Impacts of emerald ash borer-induced tree mortality on leaf litter arthropods and exotic earthworms. *Pedobiologia*, *54*(5–6), 261–265. https://doi.org/10.1016/j.pedobi.2011.05.001

van der Heyde, M., Bunce, M., Dixon, K., Fernandes, K., Majer, J., Wardell-Johnson, G., White, N., Nevill, P., & der Heyde, van. (2021). Evaluating restoration trajectories using DNA metabarcoding of invertebrates and their associated plant communities. *Authorea Preprints*. https://doi.org/10.22541/au.161383346.69785032/v1

Van Meerbeek, K., Jucker, T., & Svenning, J. C. (2021). Unifying the concepts of stability and resilience in ecology. In *Journal of Ecology* (Vol. 109, Issue 9, pp. 3114–3132). John Wiley and Sons Inc. https://doi.org/10.1111/1365-2745.13651

Vauramo, S., & Setälä, H. (2011). Decomposition of labile and recalcitrant litter types under different plant communities in urban soils. *Urban Ecosystems*, *14*(1), 59–70. https://doi.org/10.1007/s11252-010-0140-9

Viera, V. M., Viblanc, V. A., Filippi-Codaccioni, O., Côté, S. D., & Groscolas, R. (2011). Active territory defence at a low energy cost in a colonial seabird. *Animal Behaviour*, *82*(1), 69–76. https://doi.org/10.1016/j.anbehav.2011.04.001

Vigiak, O., Malagó, A., Bouraoui, F., Grizzetti, B., Weissteiner, C. J., & Pastori, M. (2016). Impact of current riparian land on sediment retention in the Danube River Basin. *Sustainability of Water Quality and Ecology*, *8*, 30–49. https://doi.org/10.1016/j.swaqe.2016.08.001

Vorel, A., Válková, L., Hamšíková, L., Maloň, J., & Korbelová, J. (2015). Beaver foraging behaviour: Seasonal foraging specialization by a choosy generalist herbivore. *Behavioral Ecology and Sociobiology*, *69*(7), 1221–1235. https://doi.org/10.1007/s00265-015-1936-7

Vought, L. B. M., Dahl, J., Lauge Pedersen, C., & Lacoursière, J. O. (1994). Nutrient Retention in riparian ecotones. *Ambio*, *23*(6), 342–348. http://www.jstor.orgURL:http://www.jstor.org/stable/4314234http://www.jstor.org/stable/4314234?seq=1&cid=pdf-reference#references_tab_contents

Waite, I. R., Herlihy, A. T., Larsen, D. P., Urquhart, N. S., & Klemm, D. J. (2004). The effects of macroinvertebrate taxonomic resolution in large landscape bioassessments: An example from the Mid-Atlantic Highlands, U.S.A. *Freshwater Biology*, *49*(4), 474–489. https://doi.org/10.1111/j.1365-2427.2004.01197.x

Wang, L., Wang, D., Liu, J., Huang, Y., & Hodgkinson, K. C. (2011). Diet selection variation of a large herbivore in a feeding experiment with increasing species numbers and different plant functional group combinations. *Acta Oecologica*, *37*(3), 263–268. https://doi.org/10.1016/j.actao.2011.02.010

Wang, X. Y., Miao, Y., Yu, S., Chen, X. Y., & Schmid, B. (2014). Genotypic diversity of an invasive plant species promotes litter decomposition and associated processes. *Oecologia*, *174*(3), 993–1005. https://doi.org/10.1007/s00442-013-2816-3

Webster, J. R., & Benfield, E. F. (1986). Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics. Vol. 17*, 567–594. https://doi.org/10.1146/annurev.es.17.110186.003031

Wipfli, M. S. (1997). Terrestrial invertebrates as salmonid prey andnitrogen sources in streams: contrastingold-growth and young-growth riparian forests insoutheastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 1259–1269.

Wood, J. L. A., Grant, J. W. A., & Belanger, M. H. (2012). Population density and territory size in juvenile rainbow trout, Oncorhynchus mykiss: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(6), 1121–1128. https://doi.org/10.1139/F2012-048

www.canada.ca. (2022, June 15). https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/black-ash-2018.html

www.fs.fed.us. (2022, June 15). https://www.fs.fed.us/nrs/atlas/tree

Wyman, R. L., & Hotaling, L. (1988). A test of the model of the economic defendability of a resource and territoriality using young Etroplus maculatus and Pelmatochromis subocellatus kribensis. *Environmental Biology of Fishes*, *21*(1), 69–76.

Xiong, Y., West, C. P., Brown, C. P., & Green, P. E. (2019). Digital image analysis of old world bluestem cover to estimate canopy development. *Agronomy Journal*, *111*(3), 1247–1253. https://doi.org/10.2134/agronj2018.08.0502

Zavyalov, N. A. (2014). Beavers (Castor fiber and Castor canadensis), the founders of habitats and phytophages. *Biology Bulletin Reviews*, *4*(2), 157–180. https://doi.org/10.1134/s207908641402008x