INFLUENCE DES PERTURBATIONS ANTHROPIQUES HISTORIQUES SUR LES
PATRONS D'INVASION DE PLANTES ET DE VERS DE TERRE NON-INDIGÈNES
DANS UNE FORÊT PRIMAIRE TEMPÉRÉE (RÉSERVE NATURELLE GAULT, MONT
ST-HILAIRE)


par


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# SOMMAIRE

De longs délais temporels peuvent exister entre les perturbations survenant à un site et les réponses des espèces de la communauté occupant ce site. Ces changements écosystémiques transitoires lents en comparaison d'une vie humaine peuvent être difficiles à détecter ou à comprendre sans la prise en compte du contexte temporel par l'utilisation de données historiques. C'est souvent le cas pour les processus d'invasion de plantes ou d'animaux non-indigènes dans les communautés forestières. Bien que les perturbations anthropiques soient reconnues pour faciliter les invasions dans ce type de communauté, des temps de latence importants peuvent tout de même survenir à chaque étape du processus. On peut donc penser que les patrons d'invasion d'un site représenteraient davantage les legs écologiques des perturbations plus anciennes que ceux des perturbations plus récentes.

Ce mémoire vise à évaluer si l'on gagne à tenir compte de l'âge des perturbations pour expliquer les invasions biologiques établies dans les sites environnants. Pour vérifier cela, nous avons inventorié l'abondance et la composition des communautés de plantes et de vers de terre non-indigènes dans 85 parcelles dispersées dans l'ensemble de la Réserve Naturelle Gault. Suite à une reconstitution fouillée de l'historique des perturbations anthropiques, nous avons comparé le pouvoir explicatif des perturbations initiées avant 1910 avec celui des perturbations survenues après 1910. Nous avons aussi pris en compte les variables environnementales reconnues comme importantes.

Les résultats suggèrent que dans les forêts de la Réserve Naturelle Gault, la présence et l'intensité des invasions de plantes et de vers de terre non-indigènes sont en premier lieu expliquées par la proximité aux perturbations anthropiques initiées il y a plus d'un siècle. Les conclusions de ce mémoire soulignent l'importance de l'utilisation d'une approche historique pour comprendre pleinement la durée des impacts écologiques des perturbations anthropiques quant à la facilitation des processus d'invasion biologique.

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# CHAPITRE 1 - INTRODUCTION GÉNÉRALE

«Puisque nous sommes incapables de ressentir directement les changements lents et que nous sommes encore plus limités dans nos habilités à interpréter leurs relations de cause à effet, les processus agissant durant plusieurs décennies demeurent cachés et résident dans ce que j'appelle le *présent invisible* »

**–** Magnuson, 1990 (traduction libre)

Le monde naturel n'est pas statique. Il est connu depuis longtemps que les communautés écologiques sont foncièrement dynamiques et qu'un roulement des espèces s'effectue à travers le temps et l'espace (Darwin ,1859; MacArthur et Wilson, 1967). Toutefois, compte tenu des délais temporels plus ou moins longs survenant entre les réponses des systèmes écologiques et les perturbations naturelles ou anthropiques qui les provoquent, il peut être difficile de détecter certains changements écosystémiques transitoires lents en comparaison d'une vie humaine (p.ex. : les dépôts acides, les changements planétaires induits par la hausse de la concentration de $CO_2$ ou les invasions de plantes ou d'animaux non-indigènes) (Magnuson, 1990). En ce sens, la prise en compte du contexte temporel par l'utilisation de sources de données écologiques historiques peut s'avérer d'une grande utilité pour comprendre ces changements biologiques globaux. Malgré cela, cette approche demeure souvent sous-utilisée par les écologistes (Vellend et *al*., 2013).

## 1.1. L'utilité des données historiques pour comprendre les phénomènes écologiques

L'écologie des communautés s'attarde aux patrons de diversité, d'abondance et de composition des espèces d'une communauté se trouvant dans un lieu et un temps défini et aux processus influençant cette structure (Vellend, 2010). Lorsque l'on échantillonne une communauté à un site donné, ce que l'on obtient est son portrait présent, résultant d'un ensemble d'événements passés ayant mené à cet assemblage d'espèces plus ou moins dominantes. Ce portrait statique est loin de prendre en compte le dynamisme intrinsèque de cette communauté, en changement constant face aux événements plus ou moins importants auxquels elle est confrontée (Foster, 2000). Puisque les populations d'une communauté peuvent répondre à des changements environnementaux naturels ou anthropiques après des délais s'étendant sur des décennies, des siècles ou même davantage (Jackson et Sax, 2010; Piqueray et *al*., 2011), une approche temporelle devient nécessaire afin de bien comprendre plusieurs phénomènes écologiques.

Bien qu'il soit impossible de remonter le temps afin de savoir à quoi ressemblaient les communautés dans le passé et quelles perturbations importantes sont intervenues pour forger les communautés actuelles, il est tout de même possible de glaner dans divers documents historiques plusieurs informations pertinentes nous permettant de mettre en lumière les conséquences à long-terme des multiples moteurs de changements globaux du passé. Dans ce but, l'écologie historique utilise de façon opportuniste l'information déjà compilée dans diverses sources : cartes et photographies historiques, relevés de terrain ou de végétations effectués dans le passé, spécimens d'herbier, etc. (Flinn et Vellend, 2005; Vellend et *al*., 2013). Même si l'utilisation des données historiques demande beaucoup de temps, s'avère souvent compliquée et n'est pas exempte de limites (les traces du passé pouvant être brèves, fragmentaires ou tout simplement absentes), sa prise en compte pourrait grandement améliorer les prédictions sur l'impact futur des perturbations et changements environnementaux. Elle

pourrait même permettre de mieux bâtir les différents programmes d'aménagement ou de conservation (Magnuson, 1990; Swetnam et *al*., 1999; Foster, 2000). L'ajout d'une perspective historique aux études en écologie a entre autre contribué substantiellement à la compréhension des effets écologiques des activités anthropiques sur les écosystèmes permettant de réaliser que les sites naturels comportent souvent une histoire culturelle beaucoup plus importante que ce que l'on assumait, où des legs de l'influence humaine passée peuvent s'avérer étonnamment persistants (Foster et *al*., 2003; Josefsson et *al*., 2009).

## 1.2. L'impact à long-terme des perturbations sur les écosystèmes

Les perturbations locales naturelles ou anthropiques peuvent altérer profondément l'habitat d'une communauté et cela dans un temps relativement court (Pickett et White, 1985; Adriens et *al*., 2006.). Avec ces dernières, on s'attend à ce que des bouleversements surviennent dans la communauté touchée se traduisant par des déclins en abondance de certaines espèces en même temps que d'autres augmentent en abondance ou colonisent en provenance d'ailleurs (Grime, 2006). À l'opposé des perturbations qui sont souvent rapides, ces réponses sous-jacentes peuvent être relativement lentes et la communauté touchée peut donc rester dans un état de déséquilibre transitoire durant un temps relativement long engendrant des délais temporels plus ou moins substantiels entre les deux processus (Piqueray et *al*., 2011; Vellend et *al*., 2013). Compte tenu de ce décalage temporel, la distribution des espèces d'une communauté peut s'avérer davantage le reflet de la configuration historique du paysage que de celle présente (Adriens et *al*., 2006).

Le concept de « legs écologiques » a récemment émergé pour traduire cette influence des évènements passés sur la structure ou la composition des écosystèmes actuels (Moorhead et *al*., 1999). L'occurrence de ces « legs historiques » a été démontrée dans plusieurs types d'écosystèmes, dans différentes régions du globe et sur différentes échelles temporelles. Par

exemple, dans les communautés forestières du continent américain, bien que plusieurs « legs écologiques » seraient le résultat de la déforestation et des pratiques agricoles datant de la colonisation européenne, d'autres tireraient leurs origines dans des activités anthropiques précolombiennes remontant à aussi loin que 700 à 1000 ans (Swetnam et *al*., 1999; Foster et *al*., 2003).

Concernant le renouvellement d'espèces d'une communauté, plusieurs concepts à saveur économique ont été proposés pour traduire les différents types de décalage temporel qui peuvent survenir entre un événement perturbateur et la réponse des espèces. Ainsi, l'expression « dette d'extinction » serait employée dans les cas où un événement causerait des extinctions d'espèces reportées à plus tard compte tenu de la capacité des espèces à persister à long-terme malgré qu'elles soient sous un seuil de survie (Tilman et *al*., 1994). Certaines études ont démontré l'existence de ces extinctions latentes suite à une détérioration ou à une fragmentation d'origine anthropique des habitats d'un écosystème. Par exemple, dans des fragments forestiers en Belgique, une « dette d'extinction » persistait plus d'un siècle après la fin de la principale phase de fragmentation forestière (Vellend et *al*., 2006). À l'opposé, un événement perturbateur pourrait aussi conduire à une colonisation inévitable à long-terme d'espèces favorisées par les nouvelles conditions environnementales créées. Un « crédit de colonisation » surviendrait alors durant le temps de latence nécessaire à la réalisation de toutes ces immigrations éventuelles (Cristofoli et *al*., 2011; Piqueray et *al*., 2011). Dans le cas où l'immigration ou l'expansion latente s'appliquerait à des espèces non-indigènes; on pourrait parler d'une « dette d'invasion » (Bennett et *al*., 2013).

## 1.3. Influence des perturbations anthropiques sur les invasions biologiques en forêt

Bien que les activités humaines soient reconnues pour augmenter l'invasibilité des communautés naturelles (Hobbs et Huenneke, 1992; Crooks, 2005), un grand décalage temporel survient souvent entre celles-ci et la colonisation d'espèces non-indigènes. En effet, avant qu'une espèce puisse coloniser avec succès un site qui lui soit approprié, celle-ci doit franchir une série d'étapes caractérisées par des temps de latence plus ou moins longs : introductions multiples de plusieurs propagules, établissement des premiers individus, survie de ceux-ci jusqu'à la maturité reproductive, persistance de la population qui en résulte; croissance de la population jusqu'à un seuil viable (Williamson et Fitter, 1996; Crooks, 2005; Jackson et Sax, 2010). Pour toutes ces raisons, la probabilité d'invasion d'un site donné serait directement proportionnelle au temps (Ricciardi, 2012) et l'assemblage des communautés façonnées par les invasions d'espèces serait donc un processus à long-terme (Bennett et *al.*, 2013).

Les écosystèmes forestiers intacts sont souvent considérés comme hautement résistants aux invasions biologiques. En réalité, cette apparence de résistance représenterait davantage une forte suppression du taux d'invasion caractérisée par des temps de latence prolongés aux différentes étapes du processus (Martin et Marks, 2006; Martin et *al.*, 2009; Essl et *al.*, 2012). Cela s'expliquerait par plusieurs caractéristiques de ces écosystèmes : la faible luminosité due à la forte fermeture du couvert; l'épaisse litière forestière agissant comme barrière physique; la relative inertie biologique due au lent taux de renouvellement des espèces et à la dominance d'espèces à longue espérance de vie, etc. (Brothers et Springarn, 1992; Bartuszevige et *al.*, 2007; Martin et *al.*, 2009). Par contre, en créant des corridors et des ouvertures facilitant l'introduction et la dispersion des propagules ainsi que l'établissement interne de populations et en diminuant l'avantage compétitif des espèces locales, les perturbations anthropiques

pourraient accélérer les processus d'invasion biologique (Von Holle et *al*., 2003; Gavier-Pizarro et *al*., 2010).

## 1.4. Impact des invasions de plantes et de vers de terre non-indigènes en forêt

Les invasions de plantes non-indigènes sont souvent considérées comme un agent de changements globaux engendrant d'importantes conséquences écologiques et économiques (Vitousek et *al*., 1996; Pimentel et *al*., 2005). En ce sens, différentes plantes non-indigènes considérées comme invasives sont reconnues pour diminuer la richesse spécifique locale ou du moins pour diminuer l'abondance d'espèces natives moins compétitives. D'autres pourraient aussi altérer les cycles des nutriments et augmenter la productivité des écosystèmes (Powell et *al*., 2011; Vilà et *al*., 2011).

Les invasions de vers de terre non-indigènes sont aussi considérées comme un agent de changement important au niveau mondial et pourrait s'avérer une menace importante à la biodiversité particulièrement dans les forêts du nord-est de l'Amérique du Nord (Hendrix et *al*., 2008; Sutherland et *al*., 2011). En effet, les vers de terre sont souvent considérés comme des « ingénieurs écosystémiques » engendrant des impacts majeurs dans les forêts qu'ils envahissent. D'abord, ils altéreraient profondément les propriétés physico-chimiques du sol : réduction ou élimination de la litière organique; modification de la composition chimique des strates et des cycles de nutriments se traduisant entre autre par une hausse du lessivage de l'azote et du phosphore (qui deviennent alors moins disponibles dans les horizons où les racines fines des herbacées sont concentrées) ; augmentation de la densité du sol ; réduction de la capacité de rétention d'eau  etc. (Scheu, 2003; Bohlen et *al*., 2004; Frelich et *al*., 2006; Hale et *al*., 2006). Ces impacts affecteraient grandement la faune du sol en diminuant entre autre l'abondance des microarthropodes et le fonctionnement des champignons mycorhiziens arbusculaires par rupture des mycélia menant à une baisse du taux de colonisation et de

l'abondance (Frelich et *al.*, 2006; Cameron et *al.*, 2013). Ces invasions tendraient aussi à simplifier et clairsemer les communautés végétales en diminuant l'abondance et la diversité des espèces natives et en favorisant la dominance de quelques espèces tolérantes (Gundale, 2002; Bohlen et *al.*, 2004; Frelich et *al.*, 2006; Holdsworth et *al.*, 2007). Les plantes invasives pourraient aussi bénéficier des nouvelles conditions environnementales et du vide laissé par les espèces natives (Nuzzo et *al.*, 2009; Eisenhauer et *al.*, 2012). Finalement, ces invasions pourraient aussi mettre en péril la régénération des arbres en menaçant sérieusement la survie des semis et l'intégrité de la banque de graines dans les sols (Frelich et *al.*, 2006).

Compte tenu des impacts potentiellement majeurs des invasions de plantes et de vers de terre non-indigènes sur les écosystèmes forestiers, il apparaît important de mieux comprendre le rôle des perturbations anthropiques dans ces invasions biologiques et la dynamique temporelle de ces lents processus. Bien qu'en Amérique du Nord, certaines études ont montré que dans les fragments forestiers, l'occurrence de plantes et de vers exotiques était souvent limitée à proximité des perturbations humaines et associée aux routes les plus anciennes (Cameron et Bayne, 2009; Jodoin et *al.*, 2008; Koncz et *al.*, 2011; Sackett et *al.*, 2012), peu d'études ont évalué implicitement l'importance de l'âge des perturbations anthropiques pour expliquer les patrons d'invasions de ces deux groupes.

## 1.5. Objectif du mémoire

Ma recherche a été menée dans la Réserve Naturelle Gault (englobant le Mont St-Hilaire, Montérégie, Québec), une large forêt primaire relativement bien préservée malgré qu'elle ait connu des perturbations anthropiques localisées importantes depuis la colonisation européenne, qui a débuté au 18$^e$ siècle. L'objectif global de ce mémoire est d'évaluer si les perturbations humaines historiques y ont laissé des empreintes importantes relatives aux patrons d'invasion biologique. Contrairement aux « dettes d'extinction » ou aux « crédits de

colonisation » associés à des espèces natives, nous pensons que les « dettes d'invasion » associées aux espèces non-indigènes devraient être plus faciles à évaluer compte tenu que l'on est assez certain que ces espèces européennes étaient absentes des communautés natives de la Réserve Naturelle Gault, avant la colonisation européenne. De plus, puisque les perturbations anthropiques les plus anciennes seraient plus à même d'avoir terminé de payer leurs « dettes d'invasion », nous pensons que les patrons d'invasion (occurrence et intensité) des plantes et des vers de terre non-indigènes devraient être expliqués par ces dernières et que, du même coup, les perturbations les plus récentes devraient avoir un faible pouvoir explicatif.

Dans le prochain chapitre, j'utiliserai une approche d'écologie historique pour recréer un portrait des perturbations anthropiques anciennes et plus récentes. Je testerai ensuite s'il y a une corrélation entre le niveau d'invasion des plantes et vers de terre non-indigènes et la distance aux perturbations anciennes (de plus d'un siècle). Dans le dernier chapitre, je ferai un retour sur les résultats et sur comment ceux-ci peuvent aider à mettre en lumière l'importance de l'approche historique pour la compréhension des processus écologiques lents tels les invasions biologiques dans les forêts primaires.

# CHAPITRE 2 - HISTORICAL ANTHROPOGENIC DISTURBANCES INFLUENCE PATTERNS OF NON-NATIVE EARTHWORM AND PLANT INVASIONS IN A TEMPERATE PRIMARY FOREST

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## 2.1. Description de l'article et contribution des auteurs

Notre article présente l'une des rares études à ce jour révélant les legs écologiques à long terme des perturbations anthropiques à la fois quant à l'invasion des vers de terres non-indigènes et quant à celle des plantes non-indigènes. La nouveauté de cette étude réside dans l'approche méthodologique utilisée pour tester l'importance des perturbations historiques dans l'explication des patrons de dispersion actuels de ces deux groupes taxonomiques. Elle réside aussi dans notre claire démonstration qu'une perspective historique est essentielle pour obtenir une pleine compréhension des invasions biologiques. Dans une vieille forêt tempérée du Québec, nous avons procédé à une reconstruction spatiale détaillée de l'historique des activités humaines. Nous avons ensuite testé le pouvoir explicatif de la proximité aux perturbations initiées à différents moments dans le passé. De façon frappante, en réponse aux perturbations les plus anciennes (c'est-à-dire celles entreprises il y a plus d'un siècle et dont les traces ne sont parfois plus du tout évidentes dans le paysage actuel), des effets importants sur les patrons d'invasion actuels des vers de terre et des plantes non-indigènes ont été révélés. Cette recherche est importante pour le domaine de la biologie de l'invasion, car elle démontre l'importance de l'utilisation d'une approche historique pour comprendre pleinement la durée des impacts écologiques dus aux perturbations anthropiques. L'article a été soumis le 10 juillet 2014 au journal Biological Invasions et a été acceptée pour publication le 08 octobre 2014.

Les cinq auteurs ont tous contribués à l'article à des degrés divers. Robin Beauséjour a élaboré la façon de tester l'importance du temps écoulé depuis l'initiation des différentes perturbations anthropiques en les séparant par périodes temporelles. Il a collecté toutes les données biologiques, environnementales et historiques, a effectué toutes les analyses et a écrit l'ensemble du manuscrit. Mark Vellend et Tanya Handa ont aussi participé à l'ensemble du processus, apportant une direction et une expertise à chaque étape. Ils ont aussi effectué plusieurs commentaires ayant engendré des modifications majeures du manuscrit. Les deux autres co-auteurs du manuscrit, Benjamin Gilbert et Martin J. Lechowicz, ont élaboré et installé le réseau de parcelles ayant été utilisé dans l'étude. Ils ont aussi fait des commentaires sur le manuscrit ayant aidé à le simplifier ou à le clarifier.

## 2.2. Abstract

Time lags are of potentially great importance during biological invasions. For example, significant delays can occur between the human activities permitting the arrival of an invader, the establishment of this new species, and the manifestation of its impacts. In this context, to assess the influence of anthropogenic disturbances, it may become necessary to include a historical perspective. In this study, we reconstructed the history of human activities in a temperate forest now protected as a nature reserve to evaluate the magnitude and duration of the impact of human disturbances (e.g., trails, old quarries), as well as environmental factors, in explaining the probability of occurrence and the intensity of invasion by non-native earthworms and plants. The present-day patterns of distribution and intensity of earthworms and plants were better explained by proximity to the oldest human disturbances (initiated more than a century ago) than by proximity to more recent disturbances or to all disturbances combined. We conclude that understanding present-day patterns of non-native species invasions may often require reconstructing the history of human disturbances that occurred decades or even centuries in the past.

## 2.3. Introduction

In the absence of long-term data, slow ecological changes can remain "invisible" to researchers, and transient phenomena occurring over decades or centuries can be impossible to fully understand (Magnuson 1990; Vellend et al. 2013). Due to the potential for extended time lags between habitat disturbance and species responses, revealing the influence of human activities on the invasion process can be difficult without adopting a historical approach (Flinn and Vellend 2005; Josefsson et al. 2009; Jackson and Sax 2010; Piqueray et al. 2011). Some important drivers of ecological changes can show substantial delays prior to measurable impacts on the ecosystem (Foster 2000). For example, there may be significant time delays between the arrival of an invasive species, the establishment of reproductive individuals and the manifestation of impacts on native communities (Crooks 2005).

Large mature temperate forests appear relatively resistant to biological invasions (Martin and Marks 2006; Essl et al. 2012). Interiors of large forest fragments have been found to be relatively weakly affected by non-native plant invasions, and occurrence of non-native plants is often limited to the edges (Theoharides and Dukes 2007; Fridley 2011; Koncz et al. 2011). Several forest characteristics have been suggested to explain this apparent invasion resistance: a dense canopy (reducing light availability), the thickness of leaf litter (acting as physical barrier to seedling establishment), and the biological inertia due to very long lifespans of the dominant species (Brothers and Spingarn 1992; Von Holle et al. 2003; Bartuszevige et al. 2007; Martin et al. 2009; Vallet et al. 2010).  In short, the seemingly high resistance to invasion of mature temperate forests may be due simply to particularly long time lags in relation to human life spans, with disturbances ultimately expected to facilitate invasion (Martin et al. 2009).

The invasibility of forest interiors by non-native plants has been shown to be increased by anthropogenic disturbances, which result in the introduction and dispersal of seeds as well as habitat modification that increases establishment success (Hobbs and Huenneke 1992; Gavier-

Pizarro et al. 2010). At the landscape scale, distance from roads and other human disturbances are often good predictors of non-native plant richness and can significantly increase the spread and establishment of non-native plants inside protected areas (Jodoin et al. 2008; Lilley and Vellend 2009; Meunier and Lavoie 2012; Pollnac et al. 2012). This process may span decades, with substantial time lags occurring, especially when habitat suitability is relatively low (Jackson and Sax 2010; Bennett et al. 2013). At our study site, the Gault Nature Reserve, Gilbert and Lechowicz (2005) found no relationship between exotic species richness and distance from present-day human disturbances (trails, reserve perimeter). However, they did not incorporate information on historical disturbances into their study and may therefore have failed to detect disturbance effects given the potential for long time lags in biotic responses.

In historically earthworm-free forests of eastern North America, invasion of European earthworms has been shown to be strongly related to human activities, which result in the introduction of propagules in new locations where subsequent establishment and spread will depend on habitat suitability (Kalisz et Dotson 1989; Suarez et al. 2006; Tiunov et al. 2006; Cameron et al. 2007). Forest interiors appear to be relatively unaffected by earthworm invasion: the probability of earthworm occurrence and the extent of spread increases as a function of proximity to roads and developments (Cameron and Bayne 2009; Sackett et al. 2012; Shartell et al. 2013). Invasion of non-native species in the family Lumbricidae tend to advance across forested landscapes in sequential waves, with epigeic species (those living in leaf litter) followed by endogeics (those living in the soil) and then anecics (those making deep vertical tunnels), with the impacts on plant communities increasing as this succession proceeds (James and Hendrix 2004; Hale et al. 2005; Holdsworth et al. 2007; Addison 2009). This sequence of invasions could be explained in part by greater reproductive capacities, colonization rates and environmental tolerance limits of the pioneer species in comparison with the later arrivals (Holdsworth et al. 2007). It has also been suggested that by altering the intact forest floor, by mixing O and mineral soil horizons, and by increasing the soil pH, the first acid-tolerant litter-dwelling (epigeic) invaders such as *Dendrobaena octaedra* and *Lumbricus rubellus* may facilitate the invasion of endogeic and anecic species, which are thought to be less acidophilic and less capable of establishing on intact forest floors (Hale et

al. 2005; Suarez et al. 2006; Tiunov et al. 2006; Addison 2009). In either case, time lags of multiple decades have been hypothesized to occur between the beginning of earthworm invasion in a local area and the development of a complex assemblage of different ecological groups including endogeic and anecic species (Hale et al. 2005; Tiunov et al. 2006; Stoscheck et al. 2012). However, few studies have taken a long-term perspective on the timing and rate of earthworm invasion at specific sites (see Larson et al. 2010).

The co-occurrence of relatively high abundances of non-native earthworms and non-native plants has been observed in many temperate forests of north-eastern North America (e.g. Kourtev et al. 1999; Nuzzo et al. 2009). This could be explained by the fact that both taxa thrive on soils with thin leaf litter and relatively high pH (Kourtev et al. 1999; Heimpel et al. 2010) and have similar human-mediated modes of dispersal. Alternatively, facilitation of non-native plant invasions by the prior establishment of endogeic and anecic earthworms has been proposed as an example of "invasional meltdown": a process by which one group of non-native species facilitates invasion by another group (Simberloff and von Holle 1999; Simberloff 2006; Heimpel et al. 2010). Endogeic and anecic earthworms could facilitate the colonization of non-native plants by creating soils with thin litter and elevated pH and nitrate availability (Kourtev et al. 1999; Nuzzo et al. 2009; Belote and Jones 2009; Heimpel et al. 2010). Introduction of large European earthworms into earthworm-free forests might also be an important driver of declines of native plants, thereby reducing competition for non-native invaders (Bohlen et al. 2004, Frelich et al. 2006, Sutherland et al. 2011).

Although the influence of human activities in heavily disturbed ecosystems is well demonstrated, fewer studies have investigated more subtle human influences in relatively pristine forest ecosystems (Jossefsson et al. 2009). In addition, while it has been suggested that the ability to predict the intensity of earthworm invasions may be improved by taking into account not only the presence of anthropogenic disturbances but also their duration (Hale et al. 2005; Tiunov et al. 2006), only a few studies have tested this hypothesis (see Cameron and Bayne 2009; Sackett et al. 2012). The goal of the present study was to test if recent and historical (initiated >100 years ago) anthropogenic disturbances had different effects on

present-day patterns of non-native plants and earthworms in a large, mature temperate forest. Specifically, we assessed (1) the relative importance of proximity to human disturbances occurring at different times in the past and of physical environmental conditions in predicting the pattern of non-native earthworm invasions, and (2) the relative importance of these same variables as well as properties of the earthworm community in predicting the pattern of non-native plant invasions. To address these questions, we reconstructed as accurately as possible the history of human disturbances inside and around our study site, the Gault Nature Reserve (Mont St.Hilaire, Qc, Canada). We predicted that because the dispersal of both earthworms and plants are often linked to human activities, the occurrence and intensity of earthworm invasion and the establishment of non-native plants would be greatest in areas close to the oldest human activities, regardless of whether those activities are ongoing in the present-day landscape. We also predicted that non-native plant establishment would be correlated with the intensity of earthworm invasion.

## 2.4. Materials and methods

2.4.1. Study area

This study was undertaken in the 10-km$^2$ Gault Nature Reserve (www.mcgill.ca/gault), which is located on one of the Monteregian hills (Mont St-Hilaire) 35 km east of Montreal, Quebec, Canada (45°32'N, 73°08'W). The reserve, which is surrounded by agricultural and suburban development, protects a primary forest dominated by *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech) and *Quercus rubra* (red oak) (Gilbert and Lechowicz 2005). The site has experienced highly localized anthropogenic disturbances since Europeans first settled the region in the 18$^{th}$ century.

2.4.2. History of human activities in the Gault Nature Reserve

The influence of people of European origin on Mont St-Hilaire and the surrounding area began around 1745 with establishment of the "Village de la Montagne" on the southern flanks of the mountain centered along the millstream draining Lake Hertel (see Appendix A for supporting references). Construction of a "Chemin de la Montagne" (a road) in 1768 accelerated conversion of the lower southern slopes to farmland. By1850, the area had about 1500 inhabitants, nine mills, three tanneries, two forges, a foundry and a distillery. Exploitation of natural resources had increased with the construction of two lime kilns and a proliferation of sugar shacks in the Lake Hertel basin on Mont St-Hilaire. Two major trails were established in this era, one a backfilled trail used to transport the limestone quarried on the north-eastern flank of the mountain to the village and the other a much used "Way of the Cross" ascending from the village to a chapel and 30-meter high cross erected on the highest peak on Mont St-Hilaire. A railway completed in 1848 increased access to the region and tourist facilities (a café, a 125-room hotel) were built around the village and on the shores of Lake Hertel in the second half of the 19th century. In the early 20th century, intrusive use of Mont St-Hilaire declined with destruction of the on-site hotel by fire, local abandonment of maple sugar production, and the increasing obsolescence of water-powered mills.

The economic downturn in the early 20th century created an opportunity that led to the protection of Mont St-Hilaire. In 1913, Andrew Gault purchased 890 hectares on Mont St-Hilaire from the Campbell family with the intention of using the property as a private forest reserve. He significantly reduced exploitation of the forest but continued to allow local people to fish in Lake Hertel and maintained a small orchard. In 1958, Gault bequeathed his property to McGill University with the restriction "…that its beauties and amenities may be preserved for all time to come". The university expanded protection efforts: cutting the orchard in the reserve in 1960; designating a conservation area closed to the public in 1968; creating the Mont St-Hilaire Nature Conservation Centre (www.centrenature.qc.ca/) in 1972; and acquiring adjacent properties to enlarge the reserve. During the second half of the 20th century, the

protected status of the reserve was strengthened by designation as a federal migratory bird sanctuary in 1960, as the first Canadian UNESCO Biosphere Reserve in 1978 and as a Nature Reserve on Private Land under Québec law in 2004. Several anthropogenic pressures nonetheless persist at the site including increasing residential development at the western side of the reserve and a steadily increasing number of visitors using a trail network that has expanded since the 1960s.

2.4.3. Site selection

In 2002, Gilbert and Lechowicz (2004) established 69 permanent vegetation plots distributed to ensure spatial and environmental representation and minimal correlation between distance and environmental similarity; to better assess near-distance effects 16 additional plots were added in 2004 within 100 meters of existing ones. Only forest sites not visually affected by ongoing human activities were chosen; areas within 15 m of the outer perimeter of the reserve or within 10 m of a trail or the shore of Lake Hertel were excluded.  These 85 plots were used in the present study (Fig. 1).
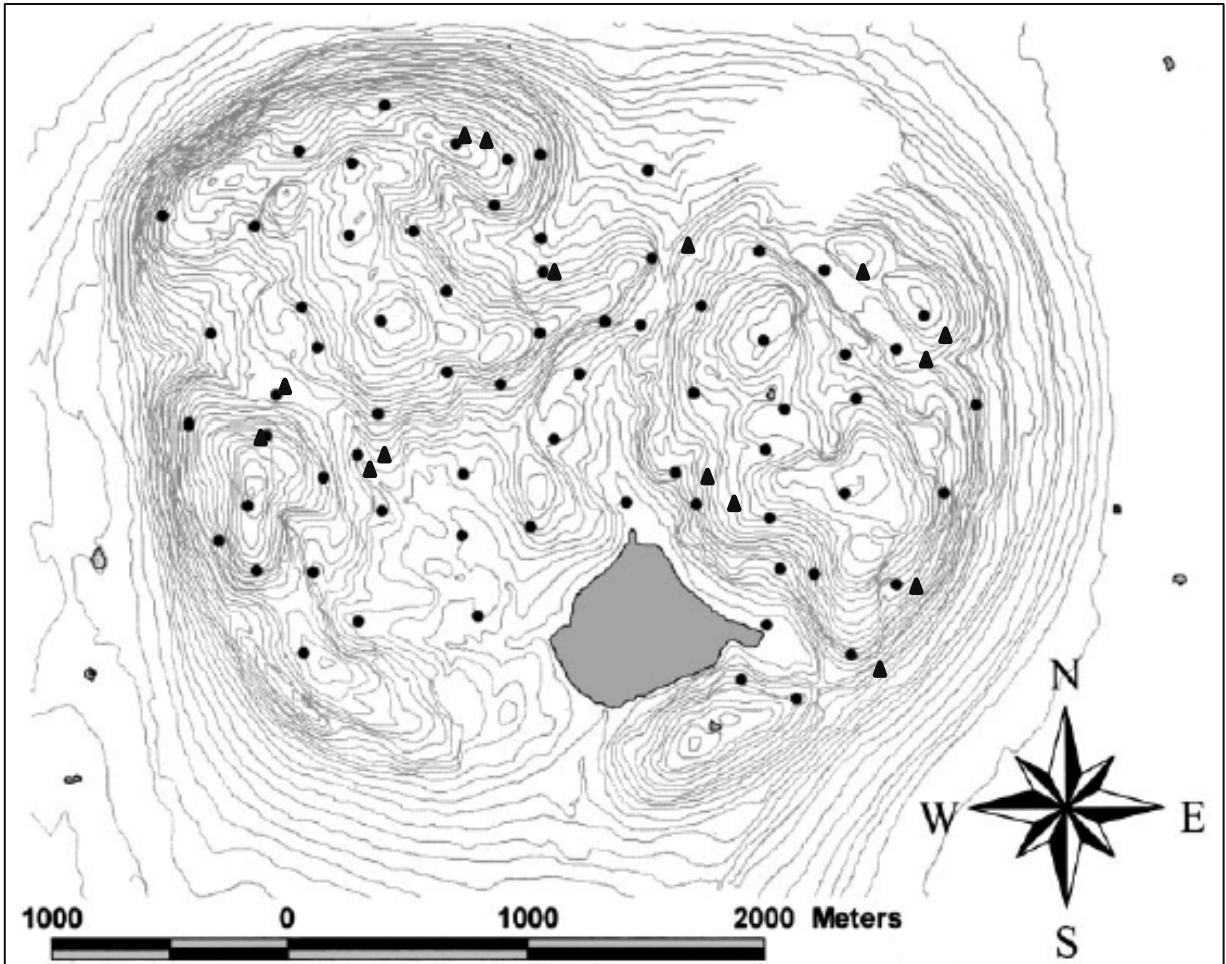
**Figure 1. Spatial distribution of sampling points. Contours are at 10-m intervals, for a total elevational gradient of 230 m over the area sampled. Map modified from Gilbert and Lechowicz (2004) (triangles represent the 16 sites added in 2004).**

2.4.4. Plant and earthworm surveys

We surveyed the understory herbaceous layer and earthworm communities at each of the 85 plots. From 6 May to 8 August 2011 – during three separate visits – percent cover of all vascular plants <1.5 m tall was estimated in 50-m$^2$ circular plots centered on a permanent marker (Gilbert and Lechowicz 2004). Nomenclature and species origins (native or non-native) follow Brouillet et al. (2010) and Lavoie et al. (2012). *Poa* species, which in vegetative condition can only be identified to the genus level, were excluded from our analyses because both native and non-native *Poa* occur on Mont St-Hilaire. With this exception we focused on the distributions and diversity of the non-native plants in the 85 study plots to draw comparisons with the factors influencing non-native earthworms.

In May 2012, we collected earthworms in four 25 cm x 25 cm quadrats at all 85 plots, with one quadrat in each cardinal direction at a distance of five meters from the permanent marker; at three sites, only 2-3 quadrats were sampled due to a lack of unsaturated soils (total number of quadrats = 336). We used the liquid-mustard extraction technique, which provides a consistent estimation of the presence and relative abundance of earthworms across a range of soils (Wironen and Moore 2006; Valckx et al. 2010; NRRI 2011). Leaf litter was first removed from the quadrat and manually sorted to search for errant earthworms. Subsequently, over a period of 20 min, two liters of 10 g/L mixture of commercial dry mustard in water was poured on the soil surface in two applications and all emerging earthworms were collected and preserved in a 70% isopropyl alcohol solution. Earthworms were identified to species (genus for the juveniles) using the key from Reynolds (1977) and uncertain individuals were sent to Dr. J.W. Reynolds of the Oligochaetology Laboratory (Kitchener, Canada) for identification.

## 2.4.5. Historical and environmental data collection

The ages and locations of human disturbances were determined using historical maps and publications (Fig.2; Appendix A and B). For analysis, disturbances were divided into those initiated either during two time periods (before and after 1910) or during four time periods (before 1845; 1846-1910; 1911-1969 and after 1969). These divisions were established to provide periods of roughly 100 or 50 years, respectively. For each site, the distance from the nearest disturbance in each category was calculated using overlays of site positions and disturbance locations in a Geographical Information System (ESRI © ArcGIS 10.0). Analyses using either two or four categories of historical disturbance yielded essentially the same results. We present only the results using two time periods: before and after 1910 (Appendix C shows the results using the separation into four periods of time).

Based on the predictors of earthworm and non-native plant invasions found in previous studies, we measured environmental variables potentially influencing the establishment of non-native earthworms and plants at the same 85 sites. We measured soil pH, presence/absence of leaf litter, slope steepness, elevation, an index of leaf litter palatability (described below) and distance from permanently wet habitats as factors relevant to earthworm invasion (Suarez et al. 2006; Tiunov et al. 2006; Wironen and Moore 2006; Shartell et al. 2013) and soil pH and moisture, slope steepness, elevation, presence/absence of leaf litter and canopy closure as factors relevant to non-native plant invasion (Rejmanez 1989; Gilbert and Lechowicz 2005; Fridley 2011; Pollnac et al. 2012). Since many authors (Kourtev et al. 1999; Nuzzo et al. 2009; Heimpel et al. 2010; Eisenhauer et al. 2012) have suggested that the presence of endogeic or anecic earthworms could favor the establishment of non-native plants, we also used this binary variable (presence/absence of earthworm invasion stage 2, described below) as a potential predictor of non-native plant invasions.

Soil pH was measured on four pooled soil cores taken in July 2012 to a depth of 8 cm. Active actidity was measured with pH meter (10 g of dry soil was mixed with 20 ml of distilled

water). To provide an index of the palatability of litter to earthworms, in 50-$m^2$ circular plots, we estimated percent cover of each tree species for the stratum >3 m and took the sum across the following species recognized to have highly palatable leaves due to high calcium content: *Acer saccharum*, *Fraxinus americana*, *Tilia americana* and *Alnus rugosa* (Hendriksen 1990; Reich et al. 2005; Tiunov et al. 2006). Distance from refugia favoring earthworm survival during drought was calculated using GIS overlays of site positions and hydrological conditions (streams, lakes, ponds) (ESRI © ArcGIS 10.0). Soil moisture in the plots was estimated from the mean of three measurements taken in July 2012 to a depth of 5 cm using a Delta-T Devices theta probe (type ML2x, Cambridge, UK). The presence of leaf litter was scored at each site in May 2012 as a binary variable: presence (regardless of thickness) or absence (bare soil). Finally, we used the Gap Light Analyzer software (Frazer et al. 1999) with hemispherical canopy photographs taken 1 m above the ground in July and August 2011 at the plot center to determine canopy openness.
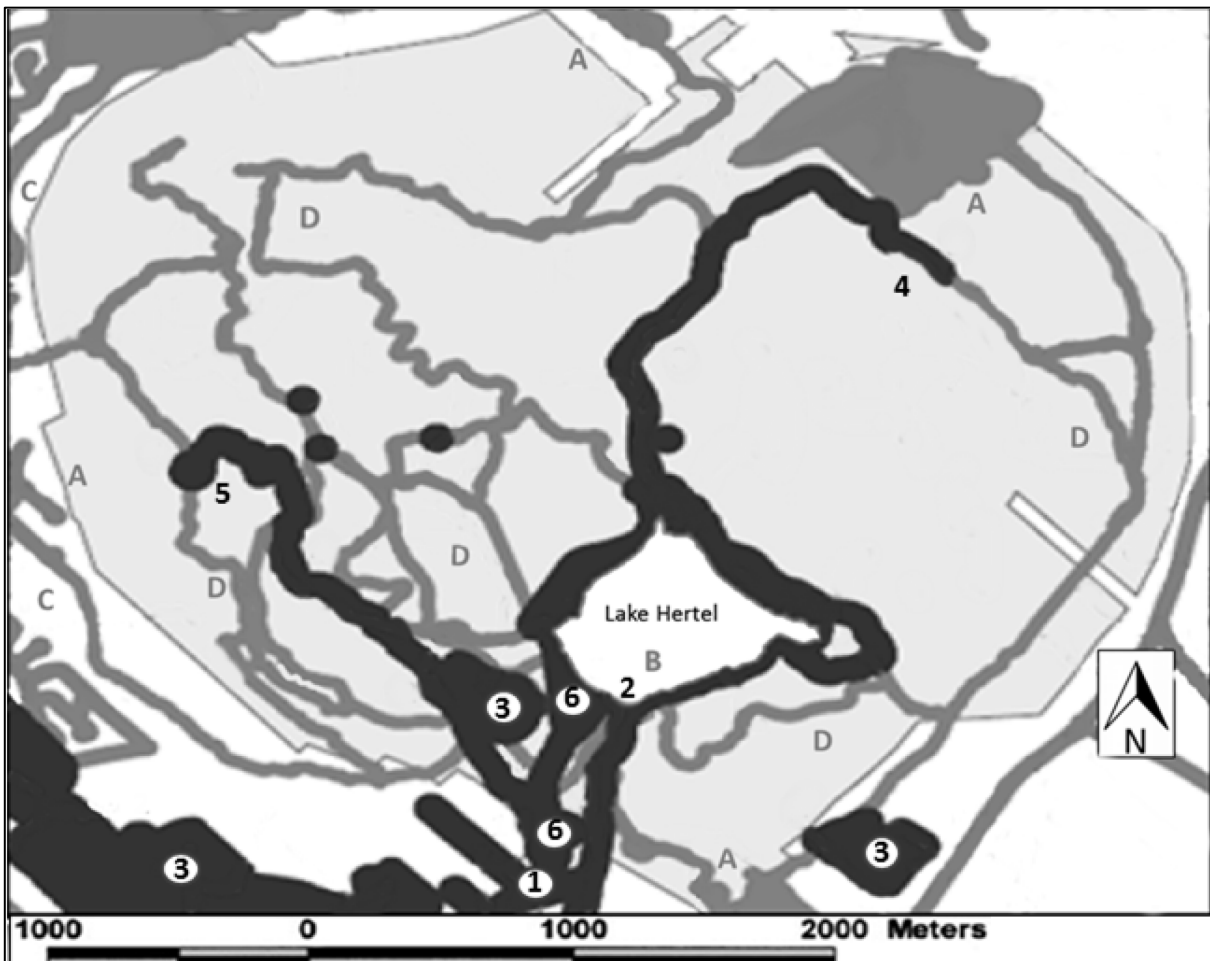
**Figure 2. Locations of the principal anthropogenic disturbances occurring inside or around the Gault Nature Reserve (whose current territory is represented in pale gray). Historical disturbances (in black) are: (1) a millstream village and (2) associated dam originating in the late 18th century; (3) orchards; (4) a 19th century lime kiln and associated backfilled trail; (5) the 19th century cross and associated trail, and (6) a 19th century hotel and café. 20th century disturbances (in dark gray) are: (A) quarries and sand pits; (B) fishing in Lake Hertel; (C) residential development and (D) the expansion of the trail network.**

2.4.6. Analyses

We quantified earthworm and plant invasions in two ways, intensity and occurrence. To characterize the intensity of earthworm invasion, sites were classified into three stages according to the presence of species or ecological groups indicative of the successional sequence typical of earthworm invasions in north-eastern American forests: 0 = earthworm-free; 1 = only epigeic or epi-endogeic species (*Dendrobaena* spp., *Lumbricus rubellus*); and 2 = presence of endogeic or anecic species (*Aporrectodea* spp., *L. terrestris*) (Addison 2009; Hale et al. 2005; Holdsworth et al. 2007). To reflect the intensity of non-native plant establishment, sites were classified into three stages according to the number of non-native species established: 0 = none; 1 = one species; and 2 = two or more species (the maximum was 4 species). Occurrence (i.e., presence vs. absence) was analyzed for several groups of interest of earthworms (epigeic or epi-endogeic species, endogeic or anecic species, and any non-native earthworms) and of non-native plants (the two main species, *Epipactis helleborine* and *Taraxacum officinale*, and any non-native plant species).

All analyses were conducted in R version 2.14.1. We used binomial logistic regressions (function clm of package ordinal (clm{ordinal}), Christensen 2012) to evaluate the ability of distance to disturbances within each time period to explain the occurrence of non-native plants and earthworms. Ordinal logistic regressions were used to predict the intensity of earthworm or plant invasion (Guisan and Harrell 2000; Jodoin et al. 2008, Meunier and Lavoie 2012). The importance of distance to disturbances during the different time periods was assessed by model ranking based on the Akaike information criterion. Each candidate model included distance to disturbance in a given time period, with all models including the environmental variables listed above (aictab{AICcmodavg}, Mazerolle 2013). For the model with the highest statistical support, Wald tests in multiple regression were used to evaluate the significance of a given proximity-to-disturbance variable and its relative importance in comparison to the environmental variables (lrm{rms}, Harrell 2013). Multicollinearity was tested using the variance inflation factor (VIF), with all VIF < 3 (Dormann et al. 2012). Assumptions about

ordinality and proportional odds were verified using plot.smean.ordinality{rms} and the goodness of fit was tested using residuals.lrm{rms} (Harrell et al. 1998; Guisan and Harrell 2000).


## 2.5. Results


A total of seven different non-native earthworm species and 13 non-native plant species occurred in our plots (Tables 1 and 2). All are of European origin. Non-native earthworms were found in 60% of the surveyed plots, with species richness ranging from 0 to 4 (median = 1). Forty percent of the plots showed the presence of only epigeic or epi-endogeic species (*Dendrobaena* spp, *Lumbricus rubellus*), and 26% of the plots showed endogeic or anecic species (*Aporrectodea* spp., *Lumbricus terrestris*). Non-native plants were present in 75% of the surveyed plots, with species richness ranging from 0 to 4 (median 1). Only two non-native species were frequent: *Epipactis helleborine* in 46% of the plots and *Taraxacum officinalis* in 54%. No non-native plants were dominant in any plot; their cover never exceeded 1%.

**Table 1. Occurrence, maximum and mean density and maximum and mean biomass of non-native earthworms. Earthworm biomass (ash-free dry mass) was estimated using length measurements and the general allometric equation of Hale et al. (2004). SD = standard deviation. Note that means ± SD are only for the subset of plots where the species in question was present.**

| Species | No. plots occupied | Maximum density (# m$^{-2}$) | Mean density (# m$^{-2}$) ± SD | Maximum biomass (g m$^{-2}$) | Mean biomass (# m$^{-2}$) ± SD |
|---|---|---|---|---|---|
| Immature *Aporrectodea* | 17 | 380 | 70.4 ± 94.1 | 2.58 | 0.71 ± 0.76 |
| *Aporrectodea rosea* | 4 | 112 | 60.3 ± 33.4 | 1.05 | 0.69 ± 0.28 |
| *Aporrectodea trapezoides* | 13 | 68 | 23.1 ± 19.9 | 3.73 | 1.49 ± 1.13 |
| *Dendrobaena octaedra* | 33 | 100 | 23.0 ± 20.4 | 1.11 | 0.18 ± 0.20 |
| *Dendrobaena rubida* | 4 | 24 | 10.0 ± 8.3 | 0.32 | 0.14 ± 0.12 |
| *Eiseniella tetraedra* | 3 | 21 | 9.8 ± 8.2 | 0.06 | 0.04 ± 0.02 |
| Immature *Lumbricus* | 13 | 60 | 25.4 ± 17.1 | 1.21 | 0.50 ± 0.40 |
| *Lumbricus rubellus* | 6 | 4 | 4.0 ± 0.0 | 0.49 | 0.31 ± 0.17 |
| *Lumbricus terrestris* | 11 | 16 | 9.3. ± 4.5 | 9.83 | 3.44 ± 2.72 |

**Table 2. Occurrence and cover of non-native plants. SD = standard deviation. Note that the mean ± SD is only for the subset of plots where the species in question was present.**

| Species | No. plots occupied | Maximum cover in any plot (%) | Mean cover (%) ± SD |
|---|---|---|---|
| Achillea millefolium | 2 | 0.1 | 0.1 ± 0 |
| Arctium lappa | 1 | 0.1 | 0.1 ± 0 |
| Barbarea vulgaris | 1 | 0.1 | 0.1 ± 0 |
| Chenopodium album | 1 | 0.1 | 0.1 ± 0 |
| Dactylis glomerata | 1 | 0.25 | 0.25 ± 0 |
| Epipactis helleborine | 39 | 0.25 | 0.13 ± 0.06 |
| Galeopsis tetrahit | 1 | 0.5 | 0.5 ± 0 |
| Geranium robertianum | 3 | 0.25 | 0.2 ± 0.07 |
| Oxalis stricta | 3 | 0.25 | 0.15 ± 0.07 |
| Taraxacum officinalis | 46 | 1 | 0.12 ± 0.13 |
| Trifolium pretense | 1 | 0.1 | 0.1 ± 0 |
| Tussilago farfara | 1 | 0.25 | 0.25 ± 0 |
| Valeriana officinalis | 2 | 0.25 | 0.18 ± 0.08 |

The occurrence of epigeic or epi-endogeic earthworm species (*Dendrobaena* spp., *Lumbricus rubellus*; Table 3a) was best predicted by the model including distance from any human disturbance; this model had an Akaike weight (Wi) of 0.84 (Wi = the probability that this model is the best among all candidate models). In this model, proximity to any human disturbance was the best predictor (P=0.0072), although elevation was also significant (Table 4a; Fig. 3a). In contrast, for the occurrence of endogeic or anecic earthworm species (Table 3b), the model including distance to historical (pre-1910) human disturbances received the strongest support (Wi of 0.94). In this model, the most significant variable was proximity to

historical human disturbances (Table 4b, P=0.0068; Fig. 3b). Only one environmental variable was also significant: the absence of leaf litter (who was associated with a greater presence of endogeic and anecic earthworms). Similarly, for all earthworm species combined (Table 3c and d), models including distance to historical human disturbances received the most support in predicting both the occurrence of invasion (Wi of 0.88) and the intensity of invasion (Wi of 0.98). For both response variables, the significant explanatory variables in the best model were the proximity to historical human disturbances, slope steepness and the absence of leaf litter (Table 4c and d; Fig. 4; Appendix D).

**Table 3. Results of multiple logistic regression models used to evaluate the relative importance of the distance from historical, recent and all human disturbances in comparison to environmental variables alone in predicting the occurrence of (a) epigeic or epi-endogeic earthworms; (b) endogeic or anecic earthworms; (c) all earthworm species and (d) the intensity of earthworm invasion in the Gault Nature Reserve (Quebec, Canada). The second-order Akaike Information Criterion (AICc), the delta AIC (Δi) and the Akaike weights (Wi) are presented for each model. Models with substantial evidence (Wi > 0.80 and Δi < 2) are in bold.  ENV represents the set of environmental variables used for either earthworms or plants (described in the Methods).**

| Models | $AIC_c$ | Δi | *Wi* |
|---|---|---|---|
| (a) Occurrence of epigeic or epi-endogeic earthworms | | | |
| Distance from historical disturbances + ENV | 121.58 | 5.78 | 0.05 |
| Distance from recent disturbances + ENV | 120.41 | 4.61 | 0.08 |
| **Distance from all disturbances + ENV** | 115.80 | 0.00 | 0.84 |
| ENV | 122.48 | 6.68 | 0.03 |
| (b) Occurrence of endogeic or anecic earthworms | | | |
| **Distance from historical disturbances + ENV** | 72.54 | 0.00 | 0.94 |
| Distance from recent disturbances + ENV | 79.77 | 7.23 | 0.03 |
| Distance from all disturbances + ENV | 82.39 | 9.85 | 0.01 |
| ENV | 79.97 | 7.42 | 0.02 |
| (c) Occurrence of any non-native earthworms | | | |
| **Distance from historical disturbances + ENV** | 104.74 | 0.00 | 0.88 |
| Distance from recent disturbances + ENV | 111.81 | 7.08 | 0.03 |
| Distance from all disturbances + ENV | 111.44 | 6.70 | 0.03 |
| ENV | 109.85 | 5.11 | 0.07 |
| (d) Intensity of earthworm invasion | | | |

| | | | |
|---|---|---|---|
| **Distance from historical disturbances + ENV** | 160.79 | 0.00 | 0.98 |
| Distance from recent disturbances + ENV | 171.51 | 10.72 | 0.00 |
| Distance from all disturbances + ENV | 171.60 | 10.81 | 0.00 |
| ENV | 169.97 | 9.18 | 0.01 |

**Table 4. Significant (P <0.05) explanatory variables in the best models from Table 1. The ordinal regression coefficient beta (β), the Z-value (Z) and the Wald test significance (P) are presented for each model.**

| Significant explanatory variables | β | Z | P |
|---|---|---|---|
| (a) Occurrence of epigeic or epi-endogeic earthworms | | | |
| Distance from any human disturbances | -0.0073 | -2.687 | 0.0072 |
| Elevation | 0.0134 | 2.026 | 0.0428 |
| (b) Occurrence of endogeic or anecic earthworms | | | |
| Distance from historical human disturbance | -0.0058 | -2.704 | 0.0068 |
| Presence of leaf litter | -2.6239 | -2.673 | 0.0075 |
| (c) Occurrence of any non-native earthworms | | | |
| Distance from historical human disturbances | -0.0033 | -2.511 | 0.0120 |
| Presence of leaf litter | -3.4679 | -2.404 | 0.0162 |
| Slope | -0.0229 | -2.187 | 0.0288 |
| (d) Intensity of earthworm invasion | | | |
| Presence of leaf litter | -2.8416 | -3.571 | 0.0004 |
| Distance from historical human disturbances | -0.0038 | -3.187 | 0.0014 |
| Slope | -0.0220 | -2.355 | 0.0185 |
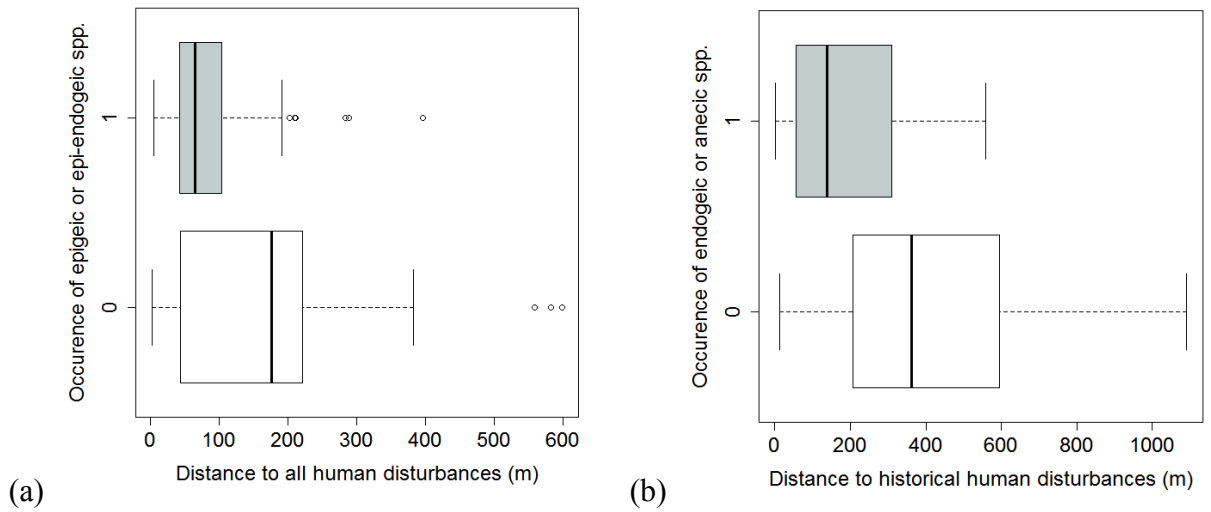
**Figure 3.** **Occurrence of epigeic or epi-endogeic earthworms (a) and occurrence of endogeic or anecic species (b) plotted against the most significant explanatory variables (box plots of raw data) in the best models predicting these variables. Sites without non-native earthworms are represented in white, and sites invaded by non-native earthworms are in pale gray.**
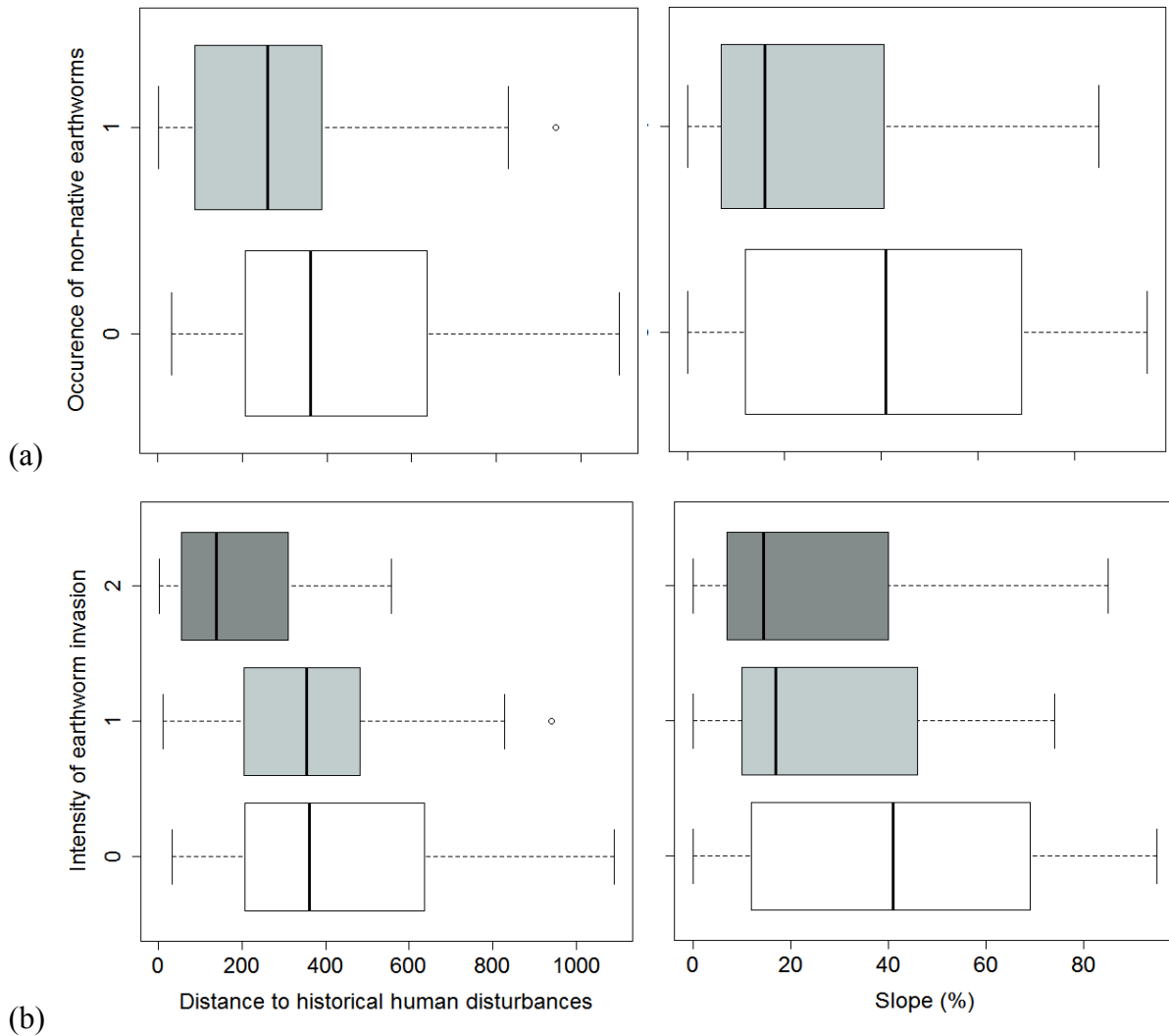
**Figure 4. Occurrence of non-native earthworms (a) or the intensity of earthworm invasion (b) plotted against the significant variables (box plots of raw data) in the best models predicting these variables. For occurrence, sites without non-native earthworms are represented in white, and sites invaded by non-native earthworms are in pale gray. For intensity, sites in stage 1 (with epigeic species) are in pale gray, and sites in stage 2 (with endogeic or anecic species) are in dark gray.**

For non-native plants, no model convincingly (i.e., with Wi > 0.80) explained either the occurrence of *E. helleborine* or the occurrence of at least one non-native plant species (Table 5a and c). In contrast, the model including distance to historical human disturbances explained the distribution of *T. officinale* with substantial support (Wi of 0.91; Table 5b). In this model, the proximity to historical human disturbances, elevation and the presence of earthworm invasion stage 2 were significant predictors (Table 6b; Appendix D). For the intensity of non-native plant invasion, the best model included proximity to historical human disturbances (Wi of 0.91; Table 5d,). In this model, the significant explanatory variables were proximity to historical human disturbances and soil pH (Table 6d; Fig. 5).

**Table 5. Results of multiple logistic regression models used to evaluate the relative importance of the distance from historical, recent and all human disturbances in comparison to environmental variables alone in predicting the occurrence of (a) *Epipactis helleborine*; (b) *Taraxacum officinalis*; (c) all non-native plants and (d) the intensity of non-native plant invasion at the Gault Nature Reserve (Quebec, Canada). The second-order Akaike Information Criterion (AICc), the delta AIC (Δi) and the Akaike weights (Wi) are presented for each model. Models with substantial evidence (Wi > 0.80 and Δi < 2) are in bold.**

| Model | AIC$_c$ | Δi | *Wi* |
|---|---|---|---|
| (a) Occurrence of *Epipactis helleborine* | | | |
| Distance from historical disturbances + ENV | 113.87 | 0.97 | 0.27 |
| Distance from recent disturbances + ENV | 115.01 | 2.11 | 0.15 |
| Distance from all disturbances + ENV | 115.31 | 2.41 | 0.13 |
| ENV | 112.90 | 0.00 | 0.44 |
| (b) Occurrence of *Taraxacum officinale* | | | |
| **Distance from historical disturbances + ENV** | 103.98 | 0.00 | 0.91 |
| Distance from recent disturbances + ENV | 111.21 | 7.22 | 0.02 |
| Distance from all disturbances + ENV | 111.89 | 7.90 | 0.02 |

| | | | |
|---|---|---|---|
| ENV | 109.67 | 5.69 | 0.05 |
| **(c) Occurrence of non-native plants** | | | |
| Distance from historical disturbances + ENV | 91.99 | 0.00 | 0.63 |
| Distance from recent disturbances + ENV | 96.19 | 4.20 | 0.08 |
| Distance from all disturbances + ENV | 96.48 | 4.48 | 0.07 |
| ENV | 94.01 | 2.02 | 0.23 |
| **(d) Intensity of non-native species richness** | | | |
| **Distance from historical disturbances + ENV** | 174.57 | 0.00 | 0.91 |
| Distance from recent disturbances + ENV | 181.30 | 6.73 | 0.03 |
| Distance from all disturbances + ENV | 181.42 | 6.85 | 0.03 |
| ENV | 181.42 | 6.85 | 0.03 |

**Table 6. Significant (P <0.05) explanatory variables in the best models from Table 5. The ordinal regression coefficient beta (β), the Z-value (Z) and the Wald test significance (P) are presented for each model.**

| Significant explicative variables | β | Z | P |
|---|---|---|---|
| (a) Occurrence of *Epipactis helleborine* | | | |
| Soil pH | 1.5634 | 2.421 | 0.0155 |
| Elevation | -0.0132 | -2.196 | 0.0281 |
| (b) Occurrence of *Taraxacum officinale* | | | |
| Elevation | 0.0222 | 2.865 | 0.0042 |
| Distance from historical human disturbances | -0.0037 | -2.645 | 0.0082 |
| Presence of earthworm invasion stage 2 | 1.9121 | 2.108 | 0.0351 |
| (c) Occurrence of non-native plants | | | |
| Soil pH | 1.9735 | 2.265 | 0.0235 |
| Distance from historical human disturbances | -0.0029 | -2.051 | 0.0402 |
| (d) Intensity of non-native species richness | | | |
| Soil pH | 1.6478 | 2.776 | 0.0055 |
| Distance from historical human disturbances | -0.0026 | -2.558 | 0.0105 |
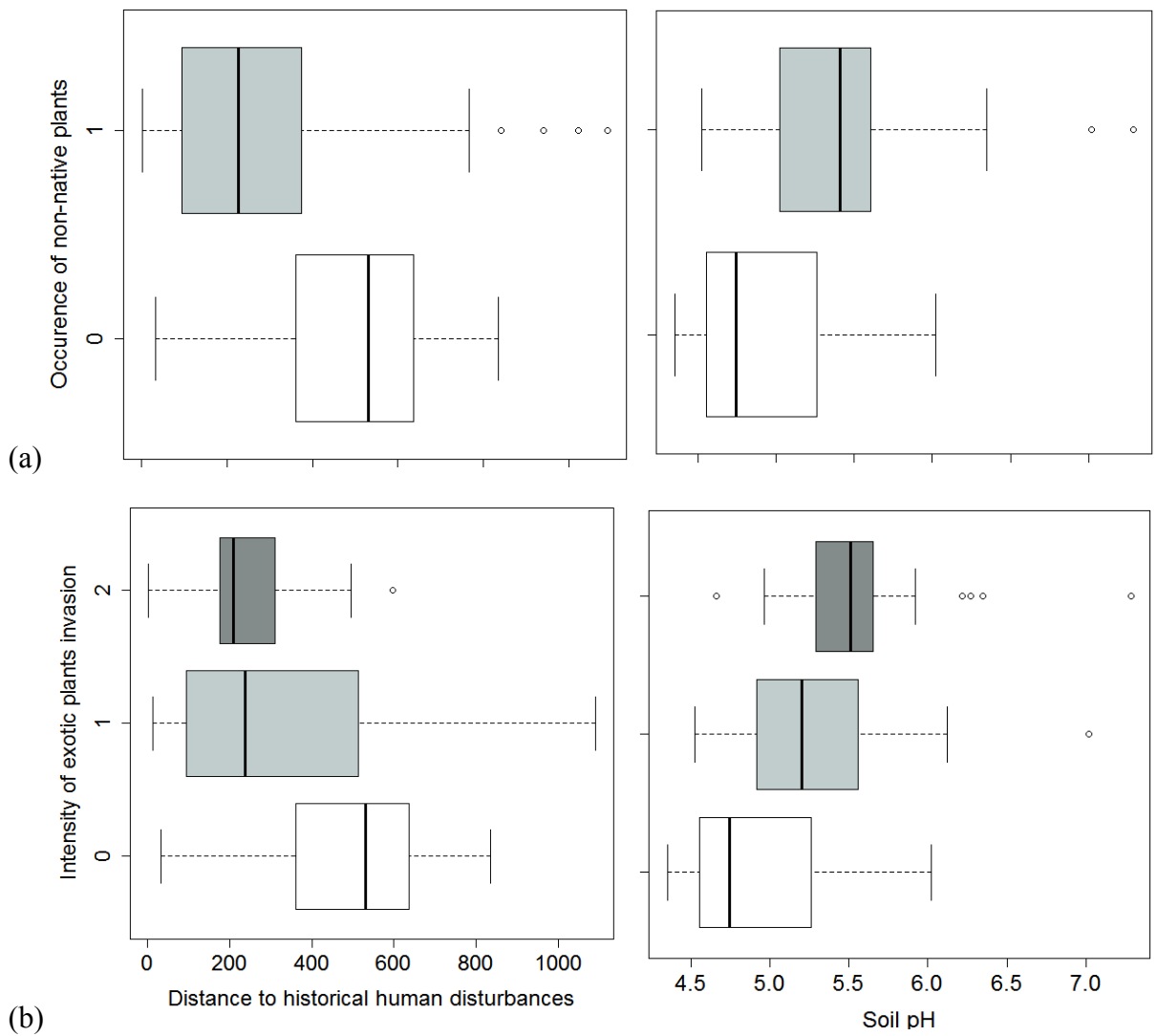
**Figure 5. Occurrence of non-native plants (a), and the intensity of non-native plant invasion (b) plotted against significant variables (box plots of raw data) in the best model predicting these variables. For occurrence, sites without non-native plants are represented in white, and sites invaded by non-native plants are in pale gray. For intensity, sites in stage 1 (with just one species) are in pale gray, and sites in stage 2 (with more than one species) are in dark gray**

## 2.6. Discussion

Although significant anthropogenic disturbance undoubtedly has occurred in the Gault Nature Reserve for more than 150 years, non-native earthworms and plants are still absent from parts of the reserve: in 40% and 25% of our study plots, respectively. While distance from recent disturbances was not a significant predictor of non-native earthworms and plants, distance from human disturbances older than a century was significantly associated with the distribution of both taxa. Only the occurrence of the earthworms in the genus *Dendrobaena* and *Lumbricus rubellus* (characteristic of early successional development in earthworm communities) showed some association with recent disturbance. Our results provide clear evidence that to predict present-day distributions of non-native species it can be important to consider not only the spatial distribution of human disturbance but also the time frame in which the disturbance was prevalent. Some of the oldest disturbances at our study site are scarcely evident in the field at present, yet their influence persists to the present day. Previous research on non-native plants using the same plots (Gilbert & Lechowicz 2005) did not consider this potential impact of proximity to past human disturbances as a factor mediating present day species distributions.

The importance of human disturbances and environmental variables varied among different ecological types of non-native earthworms. Specifically, the epigeic genus *Dendrobaena* (parthenogenic) and the epi-endogeic species *Lumbricus rubellus* were found most often in sites close to any human disturbances (i.e., regardless of age) and at relatively high elevation. In contrast, the endogeic genus *Aporrectodea* and the anecic species *Lumbricus terrestris* were largely restricted to sites closest to the oldest human disturbances and in soils without leaf litter. These differences in the predictors of the distributions of ecological types are likely related to differences in species traits. The litter dwelling *Dendrobaena* spp. and *Lumbricus rubellus* are particularly tolerant to drought, cold and acidity and have high cocoon production (Addison 2009; Holdsworth et al. 2007). In addition, *Dendrobaena* spp. are parthenogenic and have smaller cocoons found in the upper leaf litter layers and are therefore particularly likely

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to be transported by humans and vehicles (Dymond et al. 1997, Cameron and Bayne 2009). All these features allow these worms to have a high colonization rate and thus to quickly establish on sites close to sites of introduction. This could explain why these species have been found in the vicinity of all human disturbances and at sites with well-drained soils at high elevation. In contrast, endogeic and anecic species are thought to have a much lower rate of colonization due to the need for sexual reproduction, lower cocoon production, and more limited environmental tolerance (Butt and Nuutinen 1998; Holdsworth et al. 2007). This could explain why species of *Apporrectodea* and *Lumbricus terrestris* were found only in association with human disturbances older than a century and at sites without thick, acidic leaf litter.

Our results clearly confirm the possibility raised by several authors (Hale et al. 2005; Tiunov et al. 2006; Sackett et al. 2012) that the duration of proximate human activities can be important in predicting the occurrence and intensity of invasion by non-native earthworms. This effect of past anthropogenic disturbances can be crucial for at least two reasons. First, earthworm propagule pressure is inversely related to the distance from sites of earthworm introduction (Holdsworth et al. 2007). For trails and any similar disturbances, the longer the duration of their use, the greater the chances of multiple introductions (Cameron et al. 2008) and the higher the propagule pressure in their surroundings. Second, even if human disturbance increases the invasibility of forest ecosystems in the short term, the spread of exotic species into proximate forest interior may involve extended time lags. For example, in a similar northern hardwood forest, no evidence of range expansion of non-native earthworms was observed at the invasion front over a decade (Stoscheck et al. 2012). According to Hale et al. (2005), it might take several decades before a site reaches a high-intensity invasion status characterized by a complete assemblage of the different ecological types of earthworms.

For non-native plants, the important predictors of occurrence also depended on the species of interest. The lack of any significant anthropogenic predictor variables for the distribution of *E. helleborine* could be explained by the fact that this generalist orchid, with extremely small and widely dispersed seeds, is well adapted to a variety of sites ranging from shady forests or

edges of woodland to a variety of anthropogenic habitats (Kolanowska 2013). Given this broad ecological niche, we would expect a relatively short lag time between its introduction and subsequent spread, and consequently no clear link with the oldest disturbances. In contrast, the distribution of *T. officinalis* was predicted by the proximity to disturbance before 1910. Unlike the individuals of *E. helleborine* observed in the field, which were frequently reproductively mature with flowers and fruits, the individuals of *T. officinale* we encountered in closed forest were almost always non-reproductive, with just a few small leaves. The fact that *T. officinale* is ubiquitous in the seed bank throughout the reserve (Leckie et al. 2000) but not represented by mature individuals could mean that the time required for the establishment of healthy populations has not yet been reached, or that most populations, away from direct disturbance, are demographic sinks.

As predicted, historical disturbance was a strong predictor of the intensity of both non-native earthworm and plant invasions. In addition, a weak positive association was found between endogeic and anecic earthworms and the most common non-native plant *Taraxacum officinalis*. Several hypotheses might explain these results. First, it has been suggested that the factors influencing earthworm invasions are more similar to those influencing plant invasions than to those influencing invasions by more mobile animals, due to reproductive and behavioral features like cocoon/seed production and diapause/seed dormancy (Hendrix et al. 2008). Many non-native earthworms and plants were introduced to North America by similar vectors (e.g. soil dumped from ship's ballast or via imported plants roots) and spread through the landscape has been facilitated by similar human activities (e.g. construction of roads and relocation of fill or horticultural materials) (Hendrix and Bohlen 2002; Bohlen et al. 2004). Secondly, both non-native plants and endogeic or anecic earthworms occupy similar habitat with bare soil and elevated pH (Kourtev et al. 1999; Nuzzo et al. 2009). Leaf litter is often thinner and soil pH often higher at the edge of human disturbances compared to undisturbed forest interiors (Kostel-Hugues et al. 1998; Vallet et al. 2010). Given that the level of human disturbance appears to be correlated with litter depth and pH, both non-native earthworms and plants could be "passengers" taking opportunistic advantage of habitat modification caused by the same human activities (MacDougall and Turkington 2005). However, because these

earthworms are able to colonize areas with abundant leaf litter and since soil and litter properties can be directly shaped by invading earthworms, they may also act more importantly as "drivers" of these habitat characteristics. Finally, some have suggested that earthworms could also be drivers of changes in regard to the facilitation of the colonization of non-native plants (Kourtev et al. 1999; Belote and Jones 2009; Heimpel et al. 2010). In fact, endogeic and anecic earthworms are recognized to be important ecosystem engineers that can profoundly alter physico-chemical soil parameters by rapidly removing forest floor materials and by increasing soil pH (Burtelow et al. 1998, Wironen and Moore 2006). Although the presence of endogeic and anecic earthworms does not correlate with non-native plants generally, it does correlate with the most widespread non-native plant species, *Taraxacum officinale*. Our data cannot resolve the causality of the association between non-native earthworms and plants, but the fact that the presence of endogeic and anecic earthworms was a significant predictor of the presence of *T. officinalis* while controlling for environmental variables suggests that these earthworms might be both "passengers" and "drivers" of environmental change.

In conclusion, our results support arguments concerning the importance of accurately reconstructing past human activities in order to fully understand the magnitude and duration of ecological impacts due to anthropogenic disturbances (Flinn and Vellend 2005; Josefsson et al. 2009). Although some historical human disturbance may be unknown or impossible to pinpoint in space or time, and therefore not included in analyses (e.g. minor selective logging far in the past), it appears that our reconstruction captured the key historical disturbances in this ecosystem. Historical disturbances that no longer occur nonetheless seem to have left an important legacy even many decades after these activities ceased. Scrutinizing maps and historical documents can reveal that sites used by humans today have been used for much longer than previously thought (e.g. the trail leading to the highest summit of the reserve or those along the western shores of Lake Hertel). The presence of mature *L. terrestris* individuals close to these trails may well be a legacy of a long history of human disturbance and visitation. Without a good characterization of the history of human activities, it would be difficult or impossible to explain the presence of the late-successional earthworms such as *L.*

*terrestris* in sites at 400 m elevation (close to the highest elevation in the reserve) or more than 1200 m from Lake Hertel. Similarly, sites invaded by two or more species of non-native plants are all proximal to these same historical disturbances. Collectively, these examples in the distribution of non-native earthworms and plants indicate that a long-term perspective is crucial to fully understanding how anthropogenic disturbances influence present-day invasion patterns in this mature forest.

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CHAPITRE 3 - DISCUSSION GÉNÉRALE ET CONCLUSION

## 3.1. Retour sur les objectifs et points saillants de l'étude

Notre objectif était d'évaluer l'importance de la durée des perturbations humaines dans les processus d'invasion biologique en forêt tempérée primaire. Nous avions émis l'hypothèse que puisque ces processus semblent particulièrement lents dans ce type d'écosystème, les perturbations anthropiques les plus anciennes seraient plus à même d'avoir terminé de payer leurs « dettes d'invasion ». Les patrons d'invasion des plantes et des vers de terre non-indigènes devraient donc être fortement corrélés à la proximité face aux plus vieilles activités humaines. Pour valider cela, nous avons d'abord effectué, à l'aide des outils historiques disponibles (cartes et documents écrits), une reconstruction fouillée de l'historique des perturbations anthropiques de la Réserve Naturelle Gault depuis la colonisation européenne jusqu'aux plus récentes activités humaines. Nous avons ensuite évalué s'il y avait correspondance entre les patrons d'invasion des plantes et des vers de terre non-indigènes et les perturbations humaines plus que centenaires ou moins que centenaires. Puisqu'à la fois l'intensité et l'occurrence des invasions des deux groupes étaient fortement corrélées aux perturbations les plus anciennes et aucunement reliées à celles plus récentes, ces résultats laissent supposer un long décalage temporel entre les perturbations humaines d'un site et la réponse des espèces non-indigènes susceptibles de coloniser ses environs. On peut donc penser que dans les forêts primaires, les « legs écologiques » et les « dettes d'invasion » reliées aux activités anthropiques localisées peuvent être particulièrement longues.

Effectivement, notre étude a démontré l'importance de prendre en compte l'âge des perturbations humaines et non seulement la distance face à ces perturbations. Contrairement à Gilbert & Lechowicz (2005), qui dans une étude similaire avaient utilisé le même réseau de parcelles et n'avaient trouvé aucun lien entre la proximité à une perturbation et la richesse spécifique non-indigène de plantes des sites, notre étude a démontré qu'en séparant les

perturbations humaines selon si elles étaient récentes ou très anciennes, un lien fort existe entre l'intensité des invasions de plantes ou de vers de terre et la distance aux perturbations les plus anciennes. Il est donc nécessaire de prendre en compte les délais temporels survenant entre les perturbations anthropiques et les réponses des espèces à ces perturbations pour bien évaluer la magnitude de l'influence de ces perturbations sur les communautés touchées. En ce sens, selon Crooks (2005), des temps de latences importants pourraient être rencontrés à chaque étape du processus d'invasion : lors de l'introduction des propagules; lors de l'établissement des premiers individus reproductifs; lors de la croissance de la population; lors de l'expansion de cette population dans les zones environnantes et lors de la réalisation des impacts de cette nouvelle espèce dans la communauté réceptive.

La connaissance de l'histoire d'un site s'avère souvent cruciale pour comprendre les processus écologiques courants, surtout si ceux-ci sont lents, se déroulant sur une échelle temporelle plus longue que celle d'une vie humaine. Notre étude se veut un autre exemple frappant de cet énoncé. L'originalité de cet article réside dans l'approche historique adoptée pour comprendre les processus d'invasion de plantes et de vers de terre historique. Le fait d'avoir dressé un portrait le plus exhaustif possible de l'historique des perturbations anthropiques survenues dans la Réserve Naturelle Gault (par un travail de recherche minutieux permettant de localiser et de dater les différentes activités), nous a ensuite permis de diviser les activités en différentes périodes de temps selon la date d'initiation des perturbations. Malgré sa simplicité, cette division a permis de tester avec efficacité l'importance du temps écoulé pour pleinement mesurer l'impact d'une perturbation anthropique.

Bien qu'il existe plusieurs articles ayant utilisé des outils historiques pour mettre en lumière l'empreinte écologique à long-terme des perturbations anthropiques quant aux patrons d'invasion des plantes non-indigènes, cette étude serait l'une des premières, sinon la première, à démontrer des legs historiques pour des activités anthropiques plus que centenaires quant aux invasions de vers de terre en Amérique du Nord. En effet, la seule autre étude à notre connaissance ayant démontré l'importance de l'âge des perturbations pour expliquer les invasions de vers de terre en Amérique du Nord comparait l'influence de routes construites

dans les années 1950-60 versus celles datant d'après 1980 (Cameron et Bayne, 2009). Contrairement à notre étude, qui a mis à jour des legs historiques pour des perturbations datant d'avant 1910 (et même d'avant 1845, lorsque les perturbations étaient divisées en 4 périodes), cette étude avait démontré des legs écologiques pour des perturbations beaucoup plus récentes. De plus, contrairement à notre étude qui a expliqué à la fois l'occurrence des vers de terre et l'intensité de l'invasion, cette étude ne s'attardait qu'à l'occurrence des vers de terre. Notre étude serait aussi à notre connaissance l'une des premières à tenter d'expliquer à l'aide des mêmes parcelles et des mêmes analyses les facteurs responsables des patrons d'invasion à la fois des vers de terre et des plantes non-indigènes.

## 3.2. Perspectives et prolongement possible du travail accompli

Bien que l'on ait démontré l'importance de l'âge des perturbations pour expliquer les invasions de vers de terre et de plantes non-indigènes, des études futures devraient évaluer l'influence d'autres paramètres des perturbations anthropiques jugés importants. Par exemple, selon Tiunov et *al*. (2006), la probabilité de trouver une espèce de vers de terre à un site est non seulement reliée à l'âge des perturbations mais aussi au type et à l'intensité de l'utilisation humaine du site. Par ailleurs, puisque les parcelles utilisées dans notre étude sont permanentes, les échantillonnages et analyses effectués au chapitre deux pourraient être répétées dans plusieurs années pour voir si le niveau d'invasion des sites à proximité des perturbations les plus récentes rejoindra le niveau actuel des perturbations les plus anciennes. De plus, ces ré-échantillonnages permettraient de vérifier si les sites à proximité des perturbations les plus anciennes ont continué à voir de nouvelles espèces non-indigènes apparaître ou si leurs « dettes d'invasion » étaient déjà complétement « payées » au moment de la présente étude.

Notre étude renforce le message qu'une connaissance de l'écologie historique nous permet de mieux comprendre les processus d'invasion biologique. Nous avons montré que dans les forêts de la Réserve Naturelle Gault, les invasions de plantes et de vers de terre non-indigènes sont en premier lieu expliquées par la proximité des perturbations anthropiques d'avant 1910. Il

semble donc exister une longue période de transition, probablement attribuable à la série de temps de latence nécessaires à chaque d'étape du processus d'invasion, avant que la colonisation des espèces non-indigènes favorisées par les perturbations anthropiques ne se concrétise. Ces informations importantes relatives à la Réserve Naturelle Gault du Mont St-Hilaire pourraient s'avérer utiles pour l'élaboration de politiques de conservation des espèces vulnérables aux invasions de plantes ou de vers de terre non-indigènes ou pour cibler les endroits les plus susceptibles de voir naître de nouveaux foyers d'invasion. Ces informations pourraient aussi aider à prendre des décisions plus éclairées sur la réalisation ou non de nouvelles activités anthropiques. Les recommandations pouvant en découler pourraient être d'intérêt pour toutes les autres forêts primaires relativement bien préservées du Sud du Québec ou du Nord-est de l'Amérique du Nord.

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ANNEXES

## APPENDIX A. Timeline of human disturbance in the Gault Nature Reserve

| Date | Human activities | (Ref.) |
|---|---|---|
| b.1600 | Territory was inhabited by the Abenakis who called Mont St. Hilaire "Wigwômadensis" (longhouse). | 1 |
| … | | |
| 1700 | The French occupation of the region began with the grants of a seigneury surrounding Mont St. Hilaire to JB Hertel de Rouville. | 1 |
| | Foundation of the "Village de la Montagne" along the southern discharge of Lake Hertel. | 2 |
| 1750 | Clearing of the lower outer flanks of the mountain begins. | |
| | Construction of "Chemin de la Montagne", which accelerated the conversion of the lower southern slopes into orchards and farmland. | 2 |
| | Construction of a dam and a mill at the southern outflow of Lake Hertel. | 1,4 |
| | The first land grants and buildings appear at the base of the mountain. | 2,3 |
| 1800 | Beginning of the introduction of European apple, plum, pear and cherry trees. | 2 |
| | First records of fishing at Lake Hertel. | 2 |
| | Expansion of orchards and sugar shacks around and on Mont St. Hilaire. | 2,3 |
| | Construction of a chapel with a cross 30 meters high on top of *Pain de sucre* with a Way of the Cross 14 stations. | 1,2,5 |
| | Construction of two lime kilns and a backfilled trail to process and | 2,6 |

| | | |
|---|---|---|
| | transport the limestone quarried on the north flank. | |
| | Inauguration of the railway bringing more tourists. | 7 |
| 1850 | Mountain village population reaches ~1500 inhabitants, 50 houses, 9 mills and many shops or factories. | 1,2 |
| | Construction of Café Campbell on the western shore of Lake Hertel. | 1,2 |
| | Peak of maple syrup production (about 40 sugar shacks connected by a network of trails). | 2,3,5, 7,8 |
| | Construction of the Iroquois Hotel (three floors, 125 rooms, stables, pools, boats and network of trails on the mountain). | 1,2 |
| | Exploitation rights granted for small granite quarries and woodlots. | 2 |
| 1900 | Gradual decline and depopulation of the *Mountain Village*. | 2 |
| | Sale of the majority of land area of Mont St. Hilaire (890 hectares) to AH Gault. | 2 |
| | Fishing, permitted by AH Gault, becomes very popular on Lake Hertel. | 2 |
| 1950 | Development of a ski jump clearing a forest area of 165x65m. | 2 |
| | The village of Mont-St-Hilaire (between the western slopes and the Richelieu River) becomes a town with more than 3,000 inhabitants (17,200 in 2010). | 11,12 |
| | Foundation of the Center for Nature and development of an expanded trail systems in the public portion of the reserve. | 2,9 |
| | Mont St. Hilaire designated a  UNESCO Biosphere Reserve . | 2,9 |
| 2000 | Fishing and swimming prohibited on Lac Hertel. | 2 |
| | Gault Nature Reserve acquires the provincially protected status of Natural Private Reserve  . | 9 |
| | Growing tourist influx reaching exceeds 125,000 visitors per year (220,000 in 2013). | 2,10 |

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**APPENDIX B. Pictures of human disturbances inside and around the Gault Nature Reserve.**


(A)
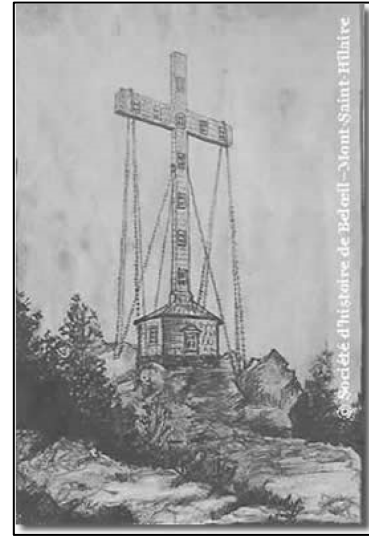

(B)


(C)


(D)


(E)
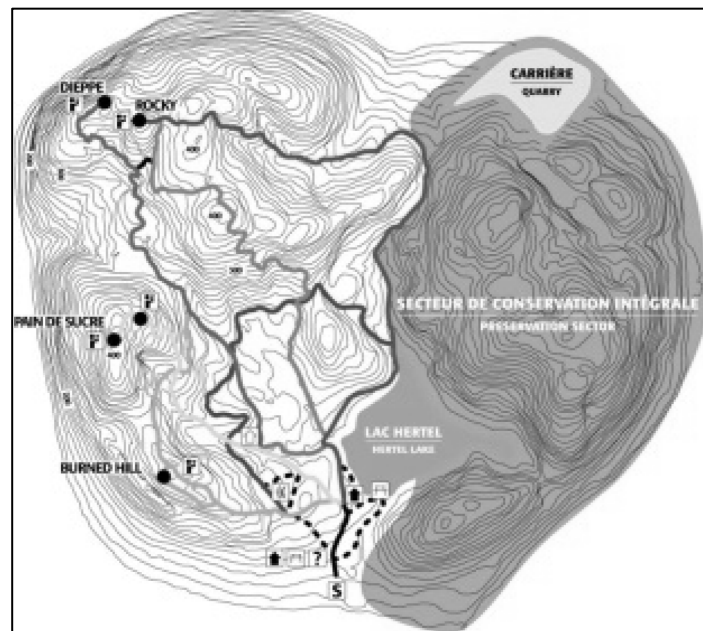
Historical disturbances are: (A) trails and sugar shacks; (B) the cross and the chapel; and (C) the hotel Iroquois. Recent disturbances are: (D) quarries; and (E) the expansion of the trail network.

**APPENDIX C. Results of analyses with disturbances categorized into four time periods.**

Results of multiple logistic regression models used to evaluate the relative importance of the distance to human disturbance (in five different periods of time) in comparison to environmental variables in explaining the occurrence of (a) epigeic or epi-endogeic earthworms.; (b) endogeic or anecic earthworms; (c) all earthworm species and (d) the intensity of earthworm invasion in the Gault Nature Reserve (Quebec, Canada). The second-order Akaike Information Criterion (AICc), the delta AIC ($\Delta i$) and the Akaike weights (Wi) are presented for each model. Models with substantial evidence (Wi > 0.80 and $\Delta i$ < 2) are in bold. ENV represents the set of environmental variables used for either earthworms or plants (described in the Methods).

| Model | $AIC_c$ | $\Delta i$ | *Wi* |
|---|---|---|---|
| (a) Occurrence of epigeic or epi-endogeic earthworms | | | |
| Distance from pre-1845 disturbances + ENV | 121.91 | 6.11 | 0.04 |
| Distance from 1846-1910 disturbances + ENV | 124.90 | 9.10 | 0.01 |
| Distance from 1911-1969 disturbances + ENV | 120.46 | 4.66 | 0.08 |
| Distance to post-1969 disturbances + ENV | 121.56 | 5.76 | 0.04 |
| **Distance from any disturbances + ENV** | 115.80 | 0.00 | 0.80 |
| ENV | 122.48 | 6.68 | 0.03 |
| (b) Occurrence of endogeic or anecic earthworms | | | |
| **Distance from pre-1845 disturbances + ENV** | 71.79 | 0.00 | 0.95 |
| Distance from 1846-1910 disturbances + ENV | 80.88 | 9.09 | 0.01 |
| Distance from 1911-1969 disturbances + ENV | 80.00 | 8.21 | 0.02 |
| Distance to post-1969 disturbances + ENV | 82.18 | 10.39 | 0.01 |
| Distance from any disturbances + ENV | 82.39 | 10.60 | 0.00 |
| ENV | 79.97 | 8.18 | 0.02 |
| (c) Occurrence of any non-native earthworms | | | |
| **Distance from pre-1845 disturbances + ENV** | 103.83 | 0.00 | 0.81 |
| Distance from 1846-1910 disturbances + ENV | 108.01 | 4.19 | 0.10 |

| Model | AICc | Δi | Wi |
|---|---|---|---|
| Distance from 1911-1969 disturbances + ENV | 111.85 | 8.02 | 0.01 |
| Distance to post-1969 disturbances + ENV | 112.20 | 8.38 | 0.01 |
| Distance from any disturbances + ENV | 111.44 | 7.61 | 0.02 |
| ENV | 109.85 | 6.02 | 0.04 |
| (d)  Intensity of earthworm invasion | | | |
| **Distance from pre-1845 disturbances + ENV** | 160.77 | 0.00 | 0.95 |
| Distance from 1846-1910 disturbances  + ENV | 168.01 | 7.23 | 0.03 |
| Distance from 1911-1969 disturbances + ENV | 171.60 | 10.83 | 0.00 |
| Distance to post-1969 disturbances + ENV | 172.42 | 11.65 | 0.00 |
| Distance from any disturbances + ENV | 171.60 | 10.83 | 0.00 |
| ENV | 169.97 | 9.20 | 0.01 |

**Results of multiple logistic regression models used to evaluate the relative importance of the distance to human disturbance (in five different periods of time) in comparison to environmental variables in explaining the occurrence of (a) of *E. helleborine* ; (b) *T. officinalis*; (c) any non-native plants and (d) the intensity of non-native plants invasion in the Gault Nature Reserve (Quebec, Canada). The second-order Akaike Information Criterion (AICc), the delta AIC (Δi) and the Akaike weights (Wi) are presented for each model. Models with substantial evidence (Wi > 0.80 and Δi < 2) are in bold. ENV represents the set of environmental variables used for either earthworms or plants (described in the Methods).**

| Model | AIC$_c$ | Δi | *Wi* |
|---|---|---|---|
| (a)  Occurrence of *Epipactis helleborine* | | | |
| Distance from pre-1845 disturbances + ENV | 114.76 | 3.66 | 0.08 |
| Distance from 1846-1910 disturbances  + ENV | 114.81 | 3.71 | 0.08 |
| Distance from 1911-1969 disturbances + ENV | 115.11 | 4.02 | 0.07 |
| Distance to post-1969 disturbances + ENV | 111.09 | 0.00 | 0.51 |
| Distance from any disturbances + ENV | 115.31 | 4.22 | 0.06 |
| ENV | 112.90 | 1.81 | 0.21 |
| (b)  Occurrence of of *Taraxacum officinale* | | | |
| Distance from pre-1845 disturbances + ENV | 105.27 | 2.06 | 0.25 |

| | | | |
|---|---|---|---|
| Distance from 1846-1910 disturbances + ENV | 103.21 | 0.00 | 0.69 |
| Distance from 1911-1969 disturbances + ENV | 111.14 | 7.93 | 0.01 |
| Distance to post-1969 disturbances + ENV | 110.92 | 7.71 | 0.01 |
| Distance from any disturbances + ENV | 111.89 | 8.68 | 0.01 |
| ENV | 109.67 | 6.46 | 0.03 |
| (c)  Occurrence of any non-native plants | | | |
| Distance from pre-1845 disturbances + ENV | 93.91 | 0.43 | 0.25 |
| Distance from 1846-1910 disturbances + ENV | 93.48 | 0.00 | 0.31 |
| Distance from 1911-1969 disturbances + ENV | 96.23 | 2.75 | 0.08 |
| Distance to post-1969 disturbances + ENV | 96.48 | 3.00 | 0.07 |
| Distance from any disturbances + ENV | 96.48 | 3.00 | 0.07 |
| ENV | 94.01 | 0.54 | 0.23 |
| (d)  Intensity of non-native plants invasion | | | |
| Distance from pre-1845 disturbances + ENV | 177.70 | 4.25 | 0.10 |
| **Distance from 1846-1910 disturbances  + ENV** | 173.45 | 0.00 | 0.81 |
| Distance from 1911-1969 disturbances + ENV | 181.35 | 7.90 | 0.02 |
| Distance to post-1969 disturbances + ENV | 181.48 | 8.03 | 0.01 |
| Distance from any disturbances + ENV | 181.42 | 7.97 | 0.02 |
| ENV | 178.99 | 5.54 | 0.05 |

**APPENDIX D. Additional figures regarding the factors influencing the non-native earthworm and plant invasion**
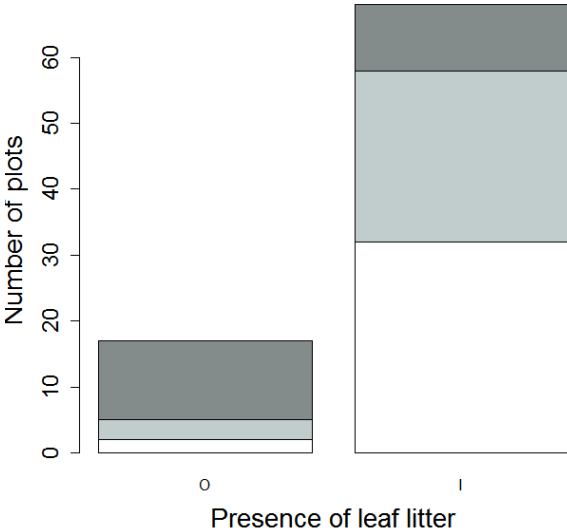


**Number of plots for each stage of non-native earthworm invasion according to the absence or presence of leaf litter. Sites without non-native earthworms are represented in white, sites of invasion stage 1 in pale gray, and sites of invasion stage 2 in dark gray.**
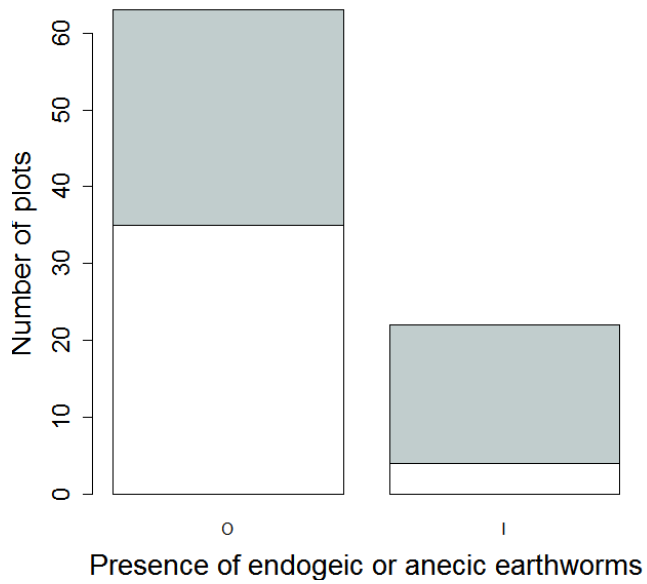
**Number of plots for presence and absence of *T. officinalis* according to the presence of endogeic or anecic earthworms. Sites without presence of *T. officinalis* are represented in white, sites with presence of *T. officinalis* in pale gray.**

**APPENDICE E. Données brutes utilisées dans les analyses**

Densité (nombre d'individus/m$^2$) des différentes espèces de vers de terre non-indigènes retrouvées en 2012 dans les 85 sites échantillonnés pour l'étude (Réserve Naturelle Gault, Québec, Canada). Légende : APO= *Apporectodea* immatures; APOROS= *Apporectodea rosea*; APOTRA= *Apporectodea trapezoides*; DENOCT= *Dendrobaena octoedra*; DENRUB= *Dendrobaena rubida;* EISTET= *Eiseniella tetraedra*; LUM= *Lumbricus* immatures; LUMRUB= *Lumbricus rubellus*; LUMTER= *Lumbricus terrestris*; Stade VE= intensité de l'invasion des vers de terre non-indigènes.

| Sites | APO | APO ROS | APO TRA | DEN OCT | DEN RUB | EIS TET | LUM | LUM RUB | LUM TER | *Stade VE* |
|-------|-----|---------|---------|---------|---------|---------|-----|---------|---------|------------|
| **B01** | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B02** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B03** | 0 | 0 | 0 | 28 | 4 | 0 | 0 | 0 | 0 | *1* |
| **B04** | 0 | 0 | 2 | 2 | 0 | 0 | 4 | 0 | 2 | *2* |
| **B05** | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B06** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B07** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B08** | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B09** | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B10** | 0 | 0 | 0 | 16 | 0 | 0 | 4 | 0 | 4 | *2* |
| **B11** | 92 | 0 | 68 | 0 | 0 | 0 | 40 | 0 | 12 | *2* |
| **B12** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B13** | 68 | 44 | 0 | 28 | 0 | 4 | 0 | 0 | 0 | *2* |
| **B14** | 0 | 0 | 8 | 0 | 0 | 4 | 20 | 0 | 0 | *2* |
| **B15** | 0 | 0 | 0 | 0 | 0 | 0 | 56 | 0 | 12 | *2* |
| **B16** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B17** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B18** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B19** | 0 | 0 | 0 | 32 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B20** | 0 | 0 | 0 | 44 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B21** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B22** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B23** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | *1* |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **B24** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B25** | 28 | 0 | 32 | 0 | 0 | 0 | 24 | 0 | 12 | *2* |
| **B26** | 60 | 0 | 48 | 0 | 0 | 0 | 24 | 0 | 8 | *2* |
| **B27** | 12 | 0 | 0 | 24 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B28** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | *1* |
| **B29** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | *1* |
| **B30** | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B31** | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 8 | *2* |
| **B32** | 20 | 0 | 12 | 8 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B33** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B34** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | *1* |
| **B35** | 24 | 0 | 4 | 0 | 0 | 0 | 32 | 0 | 4 | *2* |
| **B36** | 64 | 21 | 27 | 0 | 0 | 21 | 27 | 0 | 16 | *2* |
| **B37** | 0 | 0 | 0 | 56 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B38** | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B39** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B40** | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B41** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | *1* |
| **B42** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B43** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B44** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B45** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B46** | 240 | 112 | 0 | 44 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B47** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B48** | 64 | 0 | 4 | 0 | 0 | 0 | 60 | 4 | 16 | *2* |
| **B49** | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B50** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B51** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B52** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B53** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B54** | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B55** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B56** | 0 | 0 | 0 | 36 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B57** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B58** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B59** | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B60** | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B61** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B62** | 0 | 0 | 0 | 52 | 0 | 0 | 0 | 0 | 0 | *1* |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **B63** | 0 | 0 | 0 | 8 | 8 | 0 | 0 | 0 | 0 | *1* |
| **B64** | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B65** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B66** | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B67** | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B68** | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | *1* |
| **B69** | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | *1* |
| **B70** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B71** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B72** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B73** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B74** | 0 | 0 | 0 | 28 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B75** | 4 | 0 | 12 | 16 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B76** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B77** | 28 | 0 | 48 | 20 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B78** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B79** | 24 | 0 | 12 | 8 | 0 | 0 | 16 | 0 | 8 | *2* |
| **B80** | 380 | 64 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B81** | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B82** | 64 | 0 | 24 | 44 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B83** | 0 | 0 | 0 | 4 | 24 | 0 | 0 | 0 | 0 | *1* |
| **B84** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B85** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |

**Pourcentage de recouvrement des différentes espèces d'herbacées non-indigènes retrouvées en 2012 dans les 85 sites échantillonnés pour l'étude (Réserve Naturelle Gault, Québec, Canada). Légende : ACHMIL=** *Achillea millefolium***; ARTLAP=** *Arctium lappa***; BARVUL=** *Barbarea vulgaris***; CHEALB=** *Chenopodium album***; DACGLO=** *Dactylis glomerata***; EPIHEL=** *Epipactis helleborine***; GERROB=** *Geranium robertianum***; GALTET=** *Galeopsis tetrahit;* **OXASTR=** *Oxalis stricta***; TAROFF=** *Taraxacum officinale***; TRIPRA=** *Trifolium pratense;* **TUSFAR=** *Tussilago farfara***; VALOFF=** *Valeriana officinalis***; Stade PE= intensité de l'invasion des plantes non-indigènes.**

| Sites | ACH MIL | ARC LAP | BAR VUL | CHE ALB | DAC GLO | EPI HEL | GER ROB | GAL TET | OXA STR | TAR OFF | TRI PRA | TUS FAR | VAL OFF | *Stade PE* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **B01** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B02** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B03** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B04** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B05** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B06** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B07** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B08** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B09** | 0.1 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B10** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B11** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B12** | 0 | 0 | 0 | 0.1 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B13** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 | *2* |
| **B14** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B15** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B16** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B17** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B18** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B19** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 1 | 0 | 0.25 | 0.25 | *2* |
| **B20** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B21** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B22** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B23** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B24** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B25** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0.1 | *2* |
| **B26** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B27** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **B28** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B29** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B30** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B31** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B32** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B33** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B34** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B35** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | *2* |
| **B36** | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0.1 | 0 | 0 | 0 | *2* |
| **B37** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B38** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B39** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B40** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B41** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B42** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B43** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B44** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B45** | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B46** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B47** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B48** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B49** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B50** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B51** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B52** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B53** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B54** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B55** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B56** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B57** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B58** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B59** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B60** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | *2* |
| **B61** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B62** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B63** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B64** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B65** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B66** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B67** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **B68** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B69** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B70** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B71** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B72** | 0 | 0 | 0 | 0 | 0.25 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *2* |
| **B73** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B74** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B75** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B76** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B77** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B78** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B79** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *1* |
| **B80** | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B81** | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B82** | 0 | 0 | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |
| **B83** | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *1* |
| **B84** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | *0* |
| **B85** | 0 | 0 | 0 | 0 | 0 | 0 | 0.25 | 0 | 0 | 0.1 | 0 | 0 | 0 | *2* |

**Variables explicatives environnementales et anthropiques mesurées en 2012 dans les 85 sites échantillonnés pour l'étude (Réserve Naturelle Gault, Québec, Canada). Légende : PH= pH du sol; PE= pente (degrés); EL= élévation (m); RH= distance d'un refuge humide (m); PF= pourcentage de recouvrement des espèces d'arbres à litière palatable pour les vers de terre; LI= présence de litière importante (binaire); H= humidité du sol (%); FC= fermeture de la canopée (%); V2= présence de vers de terre endogéiques ou anéciques (binaire); AHav= distance d'une perturbation humaine initiée avant 1910 (m); AHap= distance d'une perturbation humaine initiée après 1910 (m); AH= distance de toutes perturbations humaines (m).**

| Sites | PH | PE | EL | RH | PF | LI | HU | FC | V2 | AHav | AHap | AH |
|-------|-----|-----|-----|-------|------|-----|-------|------|-----|--------|-------|-------|
| **B01** | 5.3 | 14 | 222 | 83.4 | 82.0 | 1 | 29.3 | 92.1 | 0 | 221.7 | 63.7 | 63.7 |
| **B02** | 5.6 | 74 | 186 | 115.7 | 73.0 | 0 | 6.6 | 89.9 | 0 | 766.9 | 19.4 | 19.4 |
| **B03** | 5.2 | 20 | 269 | 109.2 | 45.0 | 1 | 21.5 | 92.1 | 0 | 408.3 | 91.4 | 91.4 |
| **B04** | 5.5 | 65 | 215 | 161.1 | 63.0 | 0 | 26.6 | 91.2 | 1 | 89.0 | 118.0 | 89.0 |
| **B05** | 5.1 | 54 | 318 | 44.9 | 38.0 | 1 | 13.9 | 89.9 | 0 | 482.5 | 54.0 | 54.0 |
| **B06** | 5.2 | 4 | 221 | 5.2 | 60.0 | 1 | 100.0 | 92.3 | 0 | 42.2 | 109.4 | 42.2 |
| **B07** | 4.7 | 35 | 294 | 46.3 | 62.0 | 1 | 9.6 | 90.3 | 0 | 469.7 | 210.0 | 210.0 |
| **B08** | 5.3 | 14 | 205 | 90.0 | 8.0 | 1 | 15.9 | 88.9 | 0 | 205.8 | 119.4 | 119.4 |
| **B09** | 5.1 | 74 | 343 | 154.0 | 8.0 | 1 | 8.4 | 88.6 | 0 | 259.5 | 10.9 | 10.9 |
| **B10** | 4.6 | 7 | 399 | 291.7 | 84.0 | 1 | 12.2 | 88.8 | 1 | 28.7 | 15.4 | 15.4 |
| **B11** | 6.2 | 17 | 232 | 7.0 | 52.0 | 0 | 32.5 | 92.8 | 1 | 207.0 | 405.4 | 207.0 |
| **B12** | 5.1 | 78 | 352 | 354.3 | 16.0 | 1 | 10.1 | 92.7 | 0 | 206.8 | 90.1 | 90.1 |
| **B13** | 5.2 | 0 | 180 | 8.2 | 55.0 | 0 | 68.5 | 93.3 | 1 | 311.4 | 55.1 | 55.1 |
| **B14** | 5.8 | 0 | 184 | 2.4 | 22.0 | 1 | 100.0 | 90.8 | 1 | 2.8 | 213.5 | 2.8 |
| **B15** | 5.2 | 10 | 234 | 91.0 | 85.0 | 0 | 20.3 | 90.8 | 1 | 101.5 | 22.1 | 22.1 |
| **B16** | 6.0 | 70 | 238 | 4.3 | 50.5 | 1 | 37.9 | 89.7 | 0 | 32.6 | 13.4 | 13.4 |
| **B17** | 5.1 | 9 | 332 | 108.2 | 55.0 | 1 | 85.7 | 93.8 | 0 | 1090.7 | 184.6 | 184.6 |
| **B18** | 5.0 | 47 | 286 | 84.4 | 70.5 | 1 | 17.1 | 92.3 | 0 | 119.8 | 118.7 | 118.7 |
| **B19** | 5.5 | 6 | 236 | 5.0 | 8.0 | 1 | 100.0 | 87.5 | 0 | 12.0 | 275.9 | 12.0 |
| **B20** | 5.0 | 13 | 224 | 30.9 | 58.0 | 1 | 14.3 | 90.7 | 0 | 131.4 | 88.5 | 88.5 |
| **B21** | 5.4 | 83 | 259 | 199.7 | 29.0 | 1 | 16.2 | 88.0 | 0 | 187.0 | 180.5 | 180.5 |
| **B22** | 5.2 | 0 | 298 | 180.5 | 71.0 | 1 | 11.6 | 91.8 | 0 | 231.2 | 28.6 | 28.6 |
| **B23** | 5.0 | 13 | 314 | 98.8 | 60.0 | 1 | 17.1 | 90.0 | 0 | 381.9 | 554.7 | 381.9 |
| **B24** | 5.5 | 73 | 280 | 98.8 | 35.0 | 1 | 13.2 | 89.0 | 0 | 236.1 | 390.9 | 236.1 |
| **B25** | 5.6 | 13 | 249 | 0.7 | 55.0 | 0 | 47.6 | 91.7 | 1 | 205.7 | 274.7 | 205.7 |
| **B26** | 5.3 | 10 | 344 | 177.7 | 77.0 | 1 | 38.3 | 91.2 | 1 | 558.1 | 667.2 | 558.1 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **B27** | 4.8 | 30 | 211 | 59.2 | 47.0 | 1 | 32.9 | 90.4 | 1 | 46.3 | 303.8 | 46.3 |
| **B28** | 4.9 | 65 | 315 | 158.9 | 15.0 | 1 | 16.2 | 91.0 | 0 | 35.0 | 71.6 | 35.0 |
| **B29** | 5.4 | 15 | 356 | 96.1 | 62.0 | 1 | 20.4 | 90.4 | 0 | 614.8 | 582.1 | 582.1 |
| **B30** | 5.9 | 70 | 335 | 15.5 | 38.0 | 1 | 12.1 | 91.0 | 0 | 495.1 | 288.4 | 288.4 |
| **B31** | 4.7 | 16 | 238 | 222.3 | 15.0 | 1 | 17.1 | 89.3 | 1 | 208.0 | 165.2 | 165.2 |
| **B32** | 5.6 | 68 | 245 | 81.5 | 40.0 | 1 | 20.2 | 90.1 | 1 | 60.9 | 359.6 | 60.9 |
| **B33** | 4.8 | 0 | 390 | 176.1 | 85.0 | 1 | 12.9 | 90.5 | 0 | 598.5 | 598.9 | 598.5 |
| **B34** | 5.3 | 17 | 252 | 115.5 | 60.0 | 1 | 20.8 | 91.1 | 0 | 557.7 | 124.0 | 124.0 |
| **B35** | 7.3 | 85 | 280 | 155.7 | 79.0 | 0 | 18.7 | 90.2 | 1 | 176.8 | 336.9 | 176.8 |
| **B36** | 5.6 | 0 | 196 | 0.0 | 11.3 | 0 | 100.0 | 89.9 | 1 | 13.8 | 49.5 | 13.8 |
| **B37** | 5.5 | 27 | 333 | 109.8 | 52.0 | 0 | 100.0 | 90.2 | 0 | 712.9 | 191.0 | 191.0 |
| **B38** | 5.6 | 15 | 287 | 1.8 | 60.0 | 1 | 17.3 | 91.1 | 0 | 294.4 | 210.3 | 210.3 |
| **B39** | 5.2 | 75 | 272 | 164.5 | 50.0 | 1 | 16.4 | 90.6 | 0 | 556.9 | 201.3 | 201.3 |
| **B40** | 5.5 | 17 | 187 | 13.0 | 44.0 | 1 | 21.5 | 94.6 | 1 | 310.3 | 42.0 | 42.0 |
| **B41** | 4.7 | 65 | 345 | 140.2 | 30.0 | 1 | 13.6 | 92.1 | 0 | 125.1 | 171.6 | 125.1 |
| **B42** | 4.9 | 0 | 298 | 180.8 | 55.0 | 1 | 18.1 | 90.7 | 0 | 362.3 | 48.9 | 48.9 |
| **B43** | 5.6 | 67 | 285 | 137.7 | 55.0 | 1 | 26.2 | 91.9 | 0 | 209.6 | 177.8 | 177.8 |
| **B44** | 4.4 | 12 | 277 | 121.4 | 10.0 | 1 | 6.5 | 87.7 | 0 | 362.0 | 122.5 | 122.5 |
| **B45** | 5.0 | 47 | 320 | 247.6 | 6.0 | 1 | 10.5 | 65.2 | 0 | 1022.1 | 121.4 | 121.4 |
| **B46** | 5.6 | 7 | 247 | 6.2 | 60.0 | 0 | 47.4 | 93.9 | 1 | 69.9 | 44.8 | 44.8 |
| **B47** | 5.5 | 0 | 230 | 0.0 | 0.5 | 1 | 35.3 | 90.4 | 0 | 36.0 | 28.0 | 28.0 |
| **B48** | 5.3 | 31 | 312 | 199.9 | 69.0 | 0 | 14.9 | 90.5 | 1 | 325.9 | 24.1 | 24.1 |
| **B49** | 4.4 | 8 | 321 | 258.1 | 55.0 | 1 | 20.6 | 89.4 | 0 | 283.3 | 331.1 | 283.3 |
| **B50** | 5.8 | 95 | 273 | 139.7 | 72.0 | 1 | 10.4 | 91.4 | 0 | 842.1 | 232.1 | 232.1 |
| **B51** | 4.5 | 60 | 323 | 103.5 | 64.0 | 1 | 22.8 | 91.7 | 0 | 703.4 | 299.3 | 299.3 |
| **B52** | 4.6 | 14 | 393 | 224.9 | 12.0 | 1 | 15.4 | 90.5 | 0 | 719.8 | 176.1 | 176.1 |
| **B53** | 4.6 | 60 | 349 | 66.9 | 4.0 | 1 | 8.3 | 88.8 | 0 | 835.4 | 44.3 | 44.3 |
| **B54** | 4.8 | 0 | 376 | 179.8 | 63.3 | 1 | 13.2 | 90.8 | 0 | 395.6 | 399.6 | 395.6 |
| **B55** | 5.4 | 69 | 288 | 126.1 | 33.0 | 1 | 20.4 | 91.8 | 0 | 308.4 | 179.5 | 179.5 |
| **B56** | 5.7 | 10 | 237 | 8.9 | 19.0 | 0 | 100.0 | 93.3 | 0 | 530.3 | 41.6 | 41.6 |
| **B57** | 4.9 | 15 | 333 | 286.5 | 55.0 | 1 | 28.1 | 90.4 | 0 | 594.7 | 318.9 | 318.9 |
| **B58** | 4.7 | 70 | 292 | 107.6 | 0.0 | 1 | 10.2 | 88.9 | 0 | 729.5 | 130.8 | 130.8 |
| **B59** | 4.5 | 0 | 404 | 215.8 | 57.0 | 1 | 27.0 | 91.4 | 0 | 939.9 | 103.6 | 103.6 |
| **B60** | 5.7 | 0 | 255 | 0.0 | 20.0 | 1 | 100.0 | 94.7 | 1 | 353.2 | 26.9 | 26.9 |
| **B61** | 4.4 | 7 | 369 | 186.6 | 58.0 | 1 | 14.6 | 90.8 | 0 | 620.7 | 267.3 | 267.3 |
| **B62** | 4.5 | 0 | 410 | 274.2 | 7.0 | 1 | 100.0 | 90.3 | 0 | 454.5 | 46.1 | 46.1 |
| **B63** | 5.2 | 0 | 281 | 0.0 | 2.0 | 1 | 100.0 | 88.1 | 0 | 273.1 | 66.8 | 66.8 |
| **B64** | 4.7 | 6 | 265 | 25.8 | 70.0 | 1 | 43.0 | 94.3 | 0 | 14.3 | 93.6 | 14.3 |
| **B65** | 4.6 | 30 | 234 | 159.5 | 7.0 | 1 | 18.1 | 92.7 | 0 | 239.1 | 34.7 | 34.7 |
| **B66** | 5.5 | 32 | 319 | 23.0 | 65.0 | 1 | 28.5 | 91.9 | 0 | 828.3 | 86.6 | 86.6 |

| | | | | | | | | | | | |
|------|-----|----|-----|-------|------|---|-------|------|---|-------|-------|-------|
| **B67** | 5.7 | 31 | 307 | 89.5 | 62.0 | 1 | 19.8 | 90.7 | 0 | 323.6 | 40.2 | 40.2 |
| **B68** | 5.8 | 34 | 321 | 185.1 | 71.0 | 1 | 12.0 | 89.7 | 0 | 201.9 | 245.1 | 201.9 |
| **B69** | 5.0 | 46 | 333 | 190.6 | 18.0 | 1 | 12.0 | 89.5 | 0 | 366.9 | 617.3 | 366.9 |
| **B70** | 5.6 | 53 | 303 | 88.9 | 0.3 | 1 | 34.7 | 93.8 | 0 | 171.6 | 156.4 | 156.4 |
| **B71** | 5.3 | 14 | 285 | 12.9 | 65.0 | 1 | 45.0 | 92.6 | 0 | 261.2 | 84.4 | 84.4 |
| **B72** | 6.4 | 30 | 271 | 204.3 | 40.0 | 1 | 20.4 | 87.6 | 0 | 180.9 | 201.6 | 180.9 |
| **B73** | 5.9 | 0 | 292 | 0.0 | 55.0 | 1 | 37.8 | 93.1 | 0 | 407.4 | 255.5 | 255.5 |
| **B74** | 4.7 | 51 | 254 | 9.9 | 12.0 | 1 | 6.3 | 93.2 | 0 | 354.5 | 4.8 | 4.8 |
| **B75** | 6.3 | 0 | 254 | 0.0 | 6.0 | 1 | 100.0 | 90.0 | 1 | 360.2 | 42.0 | 42.0 |
| **B76** | 5.7 | 28 | 291 | 9.0 | 16.0 | 1 | 47.7 | 92.5 | 0 | 282.4 | 192.3 | 192.3 |
| **B77** | 7.0 | 81 | 247 | 9.9 | 0.0 | 0 | 35.3 | 92.9 | 1 | 76.1 | 68.3 | 68.3 |
| **B78** | 5.5 | 62 | 256 | 19.7 | 50.5 | 1 | 17.6 | 91.9 | 0 | 205.7 | 280.0 | 205.7 |
| **B79** | 5.2 | 40 | 289 | 162.2 | 50.0 | 1 | 10.6 | 89.1 | 1 | 210.8 | 373.2 | 210.8 |
| **B80** | 5.6 | 41 | 250 | 18.7 | 75.0 | 0 | 41.0 | 93.6 | 1 | 56.4 | 30.4 | 30.4 |
| **B81** | 5.0 | 53 | 254 | 15.1 | 70.0 | 1 | 20.0 | 93.8 | 0 | 86.5 | 66.3 | 66.3 |
| **B82** | 5.5 | 7 | 243 | 12.5 | 35.0 | 0 | 83.3 | 90.7 | 1 | 19.3 | 20.0 | 19.3 |
| **B83** | 6.1 | 21 | 259 | 108.4 | 50.0 | 0 | 100.0 | 91.8 | 0 | 409.2 | 90.4 | 90.4 |
| **B84** | 4.7 | 33 | 336 | 266.3 | 48.0 | 1 | 14.1 | 90.1 | 0 | 635.6 | 291.4 | 291.4 |
| **B85** | 4.7 | 51 | 329 | 267.4 | 64.0 | 1 | 15.2 | 91.0 | 0 | 595.8 | 299.6 | 299.6 |

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