UNIVERSITÉ DU QUÉBEC À MONTRÉAL

L'INFLUENCE DE LA COMPLEXITÉ DE LA FORÊT URBAINE SUR LES COMMUNAUTÉS DE LA MACROFAUNE DU SOL ET LES CONTRIBUTIONS DE LA NATURE ASSOCIÉES

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RÉSUMÉ

La mosaïque des infrastructures vertes urbaines offre de nombreux habitats pour les organismes qui y vivent. La macrofaune du sol est responsable de plusieurs fonctions biologiques et la conservation de leur habitat, le sol urbain, permet non seulement de favoriser la biodiversité, mais aussi de séquestrer le carbone et de diminuer le ruissellement des eaux de surface. Ce mémoire avait donc comme objectifs de (1) caractériser la macrofaune du sol, limité à l'ordre, et des propriétés du sol dans quatre types de végétation urbaine sur un gradient de complexité végétale. De plus, sur les mêmes sites, (2) d'observer la composition des communautés de fourmis et de vers de terre et de voir si au-delà de la complexité de la végétation (3) les propriétés du sol influencent ou sont influencées par ces communautés. Pour cela, un gradient de complexité de la végétation (pelouses avec et sans arbres seuls, des arbustes ornementaux et des boisés résiduels) a été utilisé dans plusieurs sites de la Ville de Montréal, Québec, Canada à l'été 2020. La macrofaune a été échantillonnée avec des pièges fosses (macroarthropodes) et avec l'extraction à la moutarde (vers de terre). La température, l'humidité, le taux d'infiltration d'eau, la matière organique et la compaction du sol ont été mesurés. La majorité des différences des propriétés du sol de la composition de la macrofaune du sol étaient entre les extrêmes de types de végétation, soit entre les pelouses sans arbres et les boisés. Pour les propriétés du sol, tous à l'exception de l'humidité, montraient des différences significatives entre les pelouses sans arbres et les boisés. Pour l'ensemble de la macrofaune du sol, aucune différence n'a été observée au niveau de la richesse moyenne d'ordre selon le type de végétation, mais certains taxons, particulièrement les araignées et vers de terre présentaient une variation de l'abondance moyenne. La distinction de la présence ou non d'arbre dans les pelouses pour les propriétés du sol et la communauté de macrofaune du sol étaient faible, mais les arbustes représentaient un entre-deux quant à ces habitats. Pour les communautés des fourmis, une distinction de la composition était aussi visible entre les boisés résiduels comparés aux pelouses, mais pas entre les arbustes et pelouses contrairement aux communautés de macrofaune identifié à l'ordre. La relation entre les fourmis et les vers de terre sur la matière organique était ambiguë en raison de la corrélation avec les types de végétation et les espèces de fourmis qui étaient plus associés aux arbres qu'au sol. L'ensemble des résultats soulève l'impact du choix et de la gestion des types de végétation en milieu urbain qui, avec les propriétés du sol, influencent la biodiversité présente sous nos pieds et dont la conservation, particulièrement des boisés urbains, doivent être une priorité face aux enjeux actuels.

Mots clés : Sols urbains, propriétés du sol, Formicidae, biodiversité urbaine, espace vert urbain

INTRODUCTION GÉNÉRALE

Le dernier rapport du GIEC indique une hausse de température à l'échelle de la planète (IPCC, 2023). Dans les milieux urbains de l'Amérique du Nord, le phénomène des ilots de chaleur et la fréquence des fortes précipitations risquent d'augmenter et d'intensifier le phénomène de ruissellement des eaux de surface (IPCC, 2023 ; United Nations Department of Economic and Social Affairs, 2022). Une méthode qui permet d'atténuer ces phénomènes est par l'aménagement du territoire par exemple en augmentant la présence de la végétation (IPCC, 2022 ; Pauleit *et al.*, 2017). La Ville de Montréal, une municipalité de taille moyenne, soit entre un et cinq millions d'habitants (United Nations, 2019), est un cas d'étude intéressant pour se pencher sur le choix de l'aménagement de la végétation urbaine. La Ville possède de nombreuses zones de végétation comme des jardins ou grands parcs, ainsi que huit parcs-nature avec comme vision de préserver des boisés dans un état sans perturbation. De plus, la Ville s'est fixé des cibles sur l'aménagement de son territoire avec l'implantation de 500 000 arbres entre 2020 et 2030, d'avoir 10% de son territoire sous aires protégées et 17% pour la région métropolitaine d'ici 2023 (Communauté métropolitaine de Montréal, 2019 ; Ville de Montréal, 2022).

La perte de la biodiversité à l'échelle mondiale est une autre préoccupation où une diminution de l'abondance et de la richesse d'espèces sont répertoriées pour de nombreux taxons (IPBES, 2019). Cette diminution d'individus et d'espèces serait expliquée par la perte d'habitat et les modifications qu'elle subit comme par les changements de température (Cardoso *et al.*, 2020 ; IPBES, 2019). En 2022, lors de la COP15 (Conférence des parties), des objectifs et cibles ont été adoptés dans la déclaration Kunming-Montréal qui mettent de l'avant l'importance de la biodiversité et que la création et la protection d'écosystème est un moyen d'agir pour contrer cette perte (Convention on Biological Diversity, 2022). Dans les cibles fixées lors de cette convention, la 11^{e} et 12^{e} retiennent l'attention. La 11^{e} se penche sur les contributions de la nature à la population via des approches écosystémiques ou des solutions basées sur la nature en agissant sur différents milieux tels que le sol et la régulation de l'eau (Convention on Biological Diversity, 2022). La 12^{e} se penche sur les zones urbaines et fortement peuplées en souhaitant une augmentation de la qualité des espaces bleus et verts via l'aménagement urbain pour favoriser la conservation de la biodiversité et de bénéficier de fonctions écosystémiques auxquelles elle participe (Convention on Biological Diversity, 2022). Ces actions incorporant la biodiversité, avec comme conséquence l'amélioration des bénéfices, telle que la présence de zones végétales, sont connues comme solutions basées sur la nature (Keeler *et al.*, 2019 ; MacKinnon *et al.*, 2008 ; Pauleit *et al.*, 2017). Un terme récurrent depuis plusieurs années est celui des infrastructures vertes qui peut désigner des milieux aménagés avec une emphase sur la végétation. Toutefois, il y a aussi une confusion autour de ce terme, car les concepts, l'échelle spatiale et les applications reliées aux infrastructures vertes diffèrent selon les disciplines impliquées. Cela peut avoir comme conséquences d'avoir des attentes sur les bénéfices plus larges que celles véritablement en jeu et entrainer une déception ou perte de confiance sur le concept (Matsler *et al.*, 2021). Matsler *et al.* (2021) s'est penché sur la question des concepts associés à ces infrastructures et en ressort trois catégories : planification urbaine, écologie urbaine et la gestion des eaux de pluie. Pour ce mémoire, le terme « infrastructure verte » sera surtout associé au concept d'écologie urbaine mettant de l'avant les fonctions écologiques et de certaines contributions de la nature (ou services écosystémiques) possible par cette infrastructure et biodiversité (Matsler *et al.*, 2021). Cette vision sera à une petite échelle spatiale de quelques mètres carrés où les structures végétales dominantes sont le point important.

Les sols supportent des activités et structures humaines et sont le terrain de croissance des végétaux qui sont la source de plusieurs fonctions écosystémiques (FAO, 2020 ; Guilland *et al.*, 2018 ; Morel *et al.*, 2015 ; O'Riordan *et al.*, 2021b ; Wall *et al.*, 2015). De plus, les sols proches de la population humaine sont affectés de plusieurs façons telles que par la grande quantité de surfaces imperméables des villes, comme l'asphalte, caractérisé par une forte compaction et une diminution de l'infiltration d'eau (O'Riordan *et al.*, 2021b). Ces infrastructures grises les rendent plus propices aux inondations après de fortes pluies (O'Riordan *et al.*, 2021b ; Woltemade, 2010). Les sols présents dans les villes sont implantés et modifiés par le génie civil pour qu'ils puissent remplir certaines fonctions, comme la croissance de végétaux ou améliorer le drainage (Guilland *et al.*, 2018 ; Morel *et al.*, 2015). L'origine et l'âge des sols dans les milieux urbains sont très vastes où dans certains cas, la couche supérieure du sol ou l'utilisation antérieure peuvent provenir d'un autre milieu, particulièrement agricole, et avoir des propriétés physicochimiques différentes comme le contenu en nutriments ou la texture (Morel *et al.*, 2015 ; Ziter et Turner, 2018). La texture des sols est un élément important pour la quantité de matière organique qu'un sol peut supporter ainsi que pour la porosité et donc sur l'infiltration d'eau (Fischer *et al.*, 2014). Actuellement, les écosystèmes terrestres emmagasinent plus de carbone atmosphérique qu'ils en émettent et l'aménagement des sols des villes constitue alors un potentiel pour contribuer à cet effet (IPCC, 2022 ; Lal *et al.*, 2021 ; O'Riordan *et al.*, 2021b). Très peu d'études sont faites sur les sols urbains, où seulement 1 % des études du sol sont réalisés en villes (Guilland et al. 2018). Les sols ont donc une importance pour plusieurs fonctions écosystémiques et pour supporter la biodiversité végétale, mais cet habitat est aussi vivant où une large biodiversité bactérienne et faunique y réside.

Pour ce mémoire, la macrofaune du sol sont les organismes ciblés, plus précisément les invertébrés de plus d'un centimètre. Ces organismes sont importants pour plusieurs fonctions biochimique et physique dans leurs écosystèmes comme la décomposition, la transformation et le transport de la matière organique et la formation et maintien des structures du sol (Creamer *et al.*, 2022 ; Guilland *et al.*, 2018 ; Handa *et al.*, 2014 ; Tresch *et al.*, 2019). Il y a une crainte que la diminution de la biodiversité affecte aussi la multifonctionnalité des écosystèmes (Faeth *et al.*, 2011 ; FAO, 2020 ; Wagg *et al.*, 2014). En milieu urbain, les arthropodes semblent présenter plus d'espèces généralistes que de spécialistes comparés aux milieux plus ruraux (Shochat *et al.*, 2006 ; Vergnes *et al.*, 2014). Un effet de sélection se ferait sentir dans les villes avec des changements physiologiques et comportementaux comparés aux espèces plus rurales (Shochat *et al.*, 2006). Les communautés d'invertébrés prédateurs des milieux urbains sont généralement composées d'individus de plus petite taille et qui supportent mieux les températures élevées que les communautés des milieux plus ruraux (Merckx *et al.*, 2018 ; Piano *et al.*, 2017). Des espèces exotiques, comme les vers de terre, sont qualifiées d'ingénieur du sol en raison de leur capacité à grandement modifier leur environnement (Craven *et al.*, 2017). Certains sont importants pour des réactions dans le sol, comme les décomposeurs pour la création et l'accessibilité des ressources (Bottinelli *et al.*, 2015 ; Jones *et al.*, 1994). Certains vont aussi modifier la structure physique par exemple par la création de macropores via des galeries (Bottinelli *et al.*, 2015 ; Colloff *et al.*, 2010 ; Jones *et al.*, 1994 ; Kotze *et al.*, 2012 ; Noreika *et al.*, 2015). Les galeries modifient plusieurs aspects dans le sol en réduisant la compaction ou en augmentation l'aération qui peut faciliter le passage de l'eau dans le sol (Bottinelli *et al.*, 2015). Cela peut être une solution contre la compaction du sol dû à la machinerie d'entretien (ex : tondeuse) ou au piétinement. Ces actions diminuent la porosité du sol et perturbent des microhabitats propices à la faune et la flore ainsi que d'augmenter le ruissellement des eaux de surface en diminuant le volume d'eau pouvant passer par le sol (Alaoui *et al.*, 2011 ; Chen *et al.*, 2014 ; Grimm *et al.*, 2008 ; Ossola *et al.*, 2015). Dans ce mémoire, les fourmis et les vers de terre sont deux taxons qui sont mis de l'avant en raison de leur capacité de créer des galeries dans le sol. Les fourmis comprennent des espèces avec une grande diversité de fonctions selon les différents milieux dans lesquelles on les retrouve. Les vers de terre sont particuliers en Amérique du Nord où la majorité est originaire d'Europe (Hendrix *et al.*, 2008 ; Phillips *et al.*, 2019a). Leur introduction dans le continent remonte à plusieurs siècles et viendrait du commerce maritime par les produits lié à l'agriculture et aux niveaux régionaux par le commerce de l'horticulture et la foresterie (Hendrix *et al.*, 2008).

La famille des fourmis (*Formicidae*) comporte des organismes avec une large aire de répartition et présent dans plusieurs habitats comme dans la canopée des arbres, le bois mort, des plantes non ligneuses ou directement dans le sol (Andersen, 2019 ; Ślipiński *et al.*, 2012 ; Uno *et al.*, 2010). Une particularité des fourmis est leur structure sociale où des variations entre espèces sur leur colonie comme la surface occupée, la présence de castes différentes, comme les ouvrières et soldates, où l'abondance à l'intérieur d'une colonie peut aller d'une dizaine à un million d'individus (Bourke, 1999 ; Schlick-Steiner *et al.*, 2006). Les fourmis des milieux urbanisés, caractérisées par des environnements plus fractionnés et une température plus élevée, auraient des traits plus territoriaux et thermophiles que des espèces apparentes de milieu rural ou forestier (Andersen, 2019 ; Clarke *et al.*, 2008 ; Lessard et Buddle, 2005 ; Nielsen *et al.*, 2014). La création des galeries par les fourmis est bien connue, mais l'ordre de grandeur présent dans un milieu reste toujours nébuleux (Bottinelli *et al.*, 2015). Dans l'étude de Del Toro *et al.* (2015), réalisée à l'aide de mésocosme avec une litière de feuilles, une hausse de température diminuait le taux de décomposition d'azote associé aux fourmis et les incitait à construire des galeries plus profondes et donc déplacer une plus importante quantité de sol. Il est même possible que de vielles galeries, par la présence antérieure de fourmis, puissent continuer à bénéficier le sol en augmentant l'infiltration de l'eau (Colloff *et al.*, 2010).

Les vers de terre sont considérés des ingénieurs du sol en raison de leur capacité à modifier la structure du sol et d'affecter plusieurs réactions dans celui-ci. La consommation, décomposition et le transport des sédiments qu'ils réalisent permettent une modification de la disponibilité des nutriments à différentes profondeurs (Bottinelli *et al.*, 2015 ; Craven *et al.*, 2017 ; Tóth *et al.*, 2020). De plus, la création de galeries permet une meilleure aération du sol et facilite le passage de l'eau (Fischer *et al.*, 2014). Tout de même, un des traits souvent propres aux vers de terre est leurs stratégies pour la création de galeries au niveau de la profondeur et du diamètre. Toutefois, la modification du sol n'est pas profitable aux espèces indigènes. Les organismes qui ont coévolué avec les vers de terre sont adaptés par leur action et peuvent y tirer des bénéfices (Ferlian *et al.*, 2018). Au contraire, d'autres espèces exotiques peuvent se voir faciliter leur introduction et propagation dans un milieu par ces changements d'habitats (Craven *et al.*, 2017 ; Ferlian *et al.*, 2018 ; Tóth *et al.*, 2020). La présence de vers de terre exotiques en Amérique du Nord est souvent accompagnée d'une réduction de la couverture végétale des espèces natives (Craven *et al.*, 2017 ; Ferlian *et al.*, 2018). Plusieurs espèces de vers de terre ont la capacité de rapidement se propager en milieu urbain, car la proximité des routes augmenterait leur propagation dans un milieu (Beauséjour *et al.*, 2015 ; Shartell *et al.*, 2013). Il ne semble pas avoir de consensus concernant l'abondance des vers de terre en milieu urbain, où des études avec différents gradients d'urbanisation obtiennent des résultats différents potentiellement en fonction des villes étudiées (Guilland *et al.*, 2018 ; Smetak *et al.*, 2007 ; Szlavecz *et al.*, 2006). Ainsi, le choix des vers de terre pour ce mémoire est aussi pour déterminer si malgré leur statut d'espèces exotiques envahissantes en Amérique du Nord, s'ils peuvent être des organismes qui offrent des contributions de la nature comme la séquestration de carbone et l'infiltration de l'eau dans le sol en milieu urbain.

La publication des rapports sur l'état de la biodiversité nécessite de nombreux recensements, mais la question de comment réaliser ces actions peut être soulevée. Une autre cible fixée lors de la COP15 est la 21^{e} qui traite des données pour les décideurs, mais aussi pour le grand public, non seulement pour la disponibilité, mais aussi qu'elle soit accessible pour y susciter la participation (Convention on Biological Diversity, 2022). Les invertébrés sont un groupe durement touché par ce constat où l'estimation de la richesse d'invertébrés connus est estimée à moins de 2% (Hochkirch *et al.*, 2021). Une des causes serait le manque de personnes impliquées (Hochkirch, 2016 ; Hochkirch *et al.*, 2021). Une solution pour la 21^{e} cible de la COP15 serait la science citoyenne. Depuis quelques années, des programmes pour la récolte de données et le suivi de populations ont émergé et des publications provenant de ces initiatives commencent aussi à être moins rares (Chandler *et al.*, 2017 ; Heberling *et al.*, 2021). Même si des discussions autour de l'utilisation des données provenant de ces plateformes ont lieu tel que sur l'exactitude des données et la standardisation des méthodes, ces programmes apportent de nombreux bénéfices permettant, en outre, la sensibilisation quant à la conservation (Bonney *et al.*, 2016 ; Kelly *et al.*, 2020 ; MacPhail et Colla, 2020). Des plateformes mondiales suivant une méthodologie commune comme Soil Biodiversity Observation Network (Soil BON) Foodweb Team, qui se concentre aussi sur la biodiversité du sol vivant ouvrent aussi la porte à de nouvelles technologies, par exemple avec le développement d'algorithmes avec l'intelligence artificielle pour simplifier l'identification d'individus échantillonnés (Potapov *et al.*, 2022). Cette approche, pourrait-elle être envisageable pour le grand public? Des initiatives de science citoyenne sur la biodiversité du sol sont déjà entamées avec par exemple la plateforme Jardibiodiv (Auclerc et Blanchart, 2019) ou le programme de suivi participatif de la Qualité biologique des sols (QUBS) (https://www.qubs.fr/), en France, allant généralement jusqu'au niveau taxonomique de l'Ordre voir même plus précis.

Tous les éléments énumérés dans les paragraphes précédents mettent de l'avant que la biodiversité de la flore et de la faune sont des éléments importants pour les contributions de la nature aux populations. L'étude de synthèse de Guilland *et al.* (2018) illustre la cascade de fonctions qui découlent de la biodiversité du sol au sein des villes et les liaisons entre ces différents éléments. La Figure 1 permet de visualiser les fonctions ciblées dans ce mémoire qui découlent de la biodiversité du sol et qui éventuellement peuvent aider à atténuer des problématiques propres au milieu urbain. Dans ce mémoire, la mesure de la matière organique et de l'infiltration d'eau sont deux indicateurs en lien à la gestion du ruissellement de surface et à la régulation du climat, des problématiques présentes en milieu urbain.

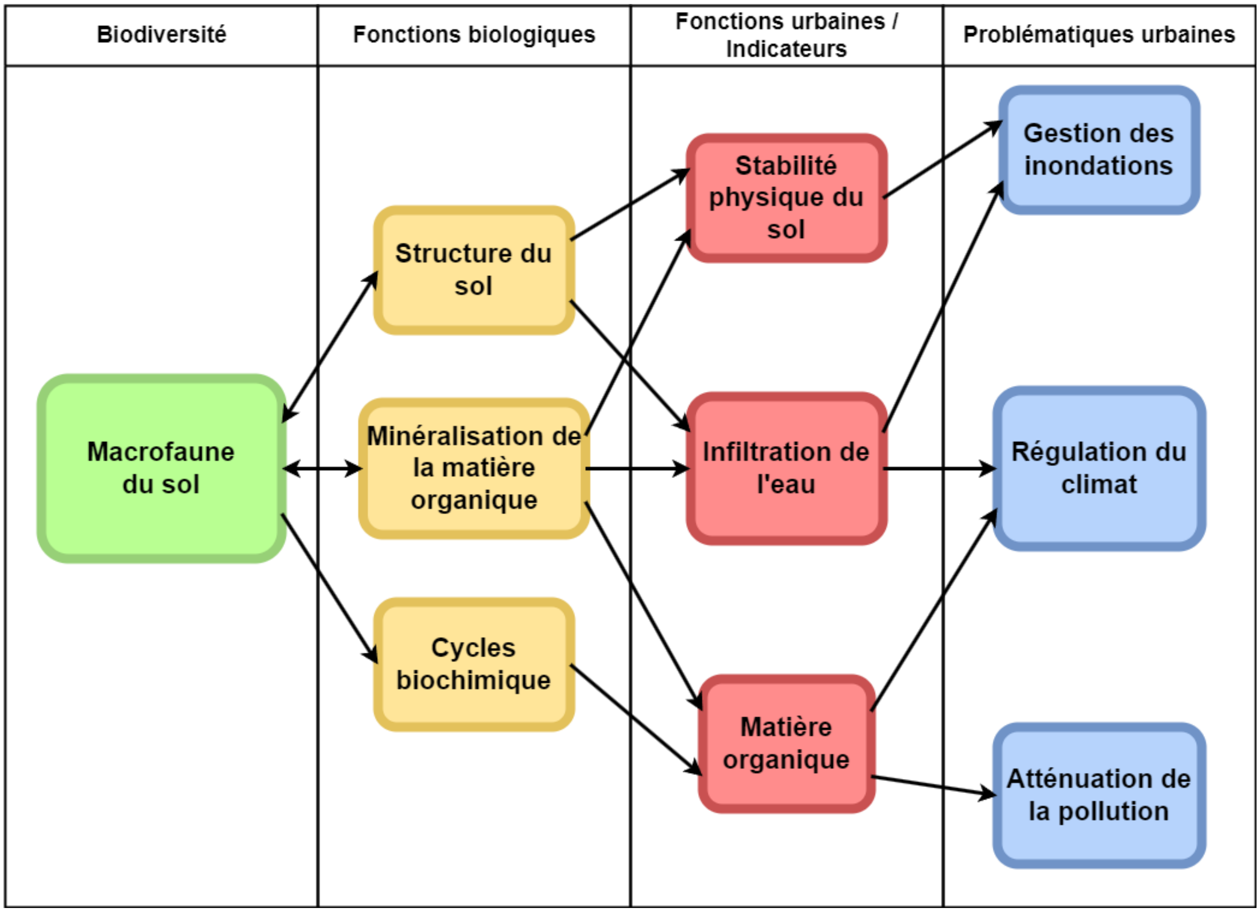

Figure 1 Représentation conceptuelle de la cascade des fonctions biologiques et urbaines découlant de la diversité de la macrofaune du sol abordée pour ce mémoire (modifié de Guilland et al. 2018).

Afin de déterminer la diversité de la macrofaune du sol en milieu urbain dans diverses infrastructures vertes et d'évaluer les effets de ces derniers sur les fonctions biologiques ciblées, quatre types de végétation de complexité différente (des pelouses sans arbres ou avec arbres isolés, des buissons ornementaux et des boisés résiduels) ont été utilisés. Les propriétés du sol mesurées étaient la matière organique, l'infiltration d'eau, l'humidité, la compaction et la température du sol. Pour aborder ces objectifs, ce mémoire est divisé en deux chapitres chacun, présenté sous la forme d'articles scientifiques en anglais, avec une différence sur le choix des taxons cibles et de la précision taxonomique. Le premier chapitre se penchera sur l'ensemble de la macrofaune du sol, mais se limitera au niveau taxonomique de l'Ordre. Cette limite taxonomique est fixée afin de vérifier si des changements et liens sont visibles même à cette précision grossière. Le deuxième chapitre utilisera les mêmes sites et la même méthodologie d'échantillonnage que la première, mais elle sera plus précise dans son exploration des communautés en utilisant un niveau taxonomique allant à l’espèce des fourmis et des vers de terre des milieux urbains. Ces deux études ont été faites sur deux campus universitaires, ainsi que dans un grand parc et des boisés dans la Ville de Montréal, Québec, Canada en été 2020. Il est attendu que les produits de ces recherches peuvent offrir un aperçu de la biodiversité du sol urbain et aussi aider à la création, à la modification et à montrer l'importance des choix d’aménagement des espaces en milieu urbain. Ces infrastructures peuvent influencer de nombreuses contributions de la nature et ils sont donc des moyens pour nous acclimater face aux changements globaux actuels et aider à répondre aux objectifs fixés par les groupes intergouvernementaux.

CHAPITRE 1

Urban forest complexity influences soil properties and soil macrofauna composition

1.1 Abstract

The vegetation composing urban forests varies in complexity from simplified lawns under sparsely isolated trees to complex residual woodlands within cities. With the increasing need of nature-based solutions to address both the climate and biodiversity crises, monitoring of a broader biodiversity in urban soils is essential. This study aimed to characterize the soil macrofauna communities and associated soil properties in four types of urban vegetation of varied complexity (lawns with and without a single tree, ornamental bushes and residual woodlands). Each of these vegetation types were studied in summer 2020 at three sites and replicated five times per site in the city of Montreal, Quebec, Canada. The soil macrofauna community was sampled with pitfall traps (macroarthropods) and mustard extraction (earthworms). Each individual was counted and identified to the order taxonomical rank. Soil was sampled to determine the amount of organic matter by loss on ignition. Soil humidity, compaction, temperature and water infiltration capacity (adjusted for soil texture assessed in the lab) were measured in the field. The overall richness of soil macrofauna order did not vary across the four different vegetation types, but lawns had a higher abundance of invertebrates compared to residual woodlands and compositional differences were observed. With the exception of humidity, soil properties were significantly different between lawns and residual woodlands. Vegetation type was a predictor for some taxa, but soil properties, particularly humidity, was a predictor for many taxa. Our results demonstrate that vegetation type in an urban setting influence the soil macrofauna biodiversity and soil properties.

1.2 Introduction

The decline of biodiversity observed in many parts of the world has increased the demand for biodiversity monitoring at a global scale (IPBES, 2019). Multiple programs of monitoring of biodiversity exist with worldwide programs like the Soil Biodiversity Observation (Soil BON), part of the Group on Earth Observations Biodiversity Observation Network (GEO BON), where a common methodology across different teams around the globe has been implemented following multiple expert meetings (Potapov *et al.*, 2022). Yet, more effort is undoubtedly necessary with evident underrepresentation in certain parts of the world where observations remain sparse and resources are limited. A solution for this situation would be to simplify taxonomical identification to attract more observers, perhaps via citizen science. Monitoring from community scientists has resulted in databases which have permitted to follow abundance trends of taxa and even associations with environmental drivers, like pollution or urbanization (Chandler *et al.*, 2017 ; Gardiner et Roy, 2022). The use of a higher taxonomical rank, like of the order, can expand the databases in more regions of the planet where reliable data is often mentioned as a barrier to the analysis coming from citizen science (MacPhail et Colla, 2020).

The wide variety of natural infrastructure types in cities provide an ideal setting to test biodiversity monitoring with size and vegetation composition that can affect the presence and abundance of animal taxa present and potentially alter associated ecosystem functions (De Deyn et Kooistra, 2021 ; Faeth *et al.*, 2011 ; Philpott *et al.*, 2014 ; Scheffers *et al.*, 2014). Soil macrofauna is an important component of the soil ecosystem and contribute to many ecosystem functions related to soil structure, litter decomposition and carbon or nitrogen biochemical cycles (Guilland *et al.*, 2018 ; Handa *et al.*, 2014 ; Kotze *et al.*, 2022 ; Tresch *et al.*, 2019). Some taxa like ants (Family: *Formicidae*), earthworms (Family: *Lumbricidae*) and ground beetles can create macropores and galleries that form new paths for water to flow and lower soil compaction that modify the physical aspect of the soil and SOM distribution (Bottinelli *et al.*, 2015 ; Colloff *et al.*, 2010 ; Kotze *et al.*, 2012 ; Noreika *et al.*, 2015 ; O'Riordan *et al.*, 2021b). The abundance of species is globally in decline (IPBES, 2019) and cities may not be an exception to this trend (Piano *et al.*, 2020 ; Saari *et al.*, 2016 ; Vergnes *et al.*, 2014). For some invertebrates in cities like spiders or ground beetle, taxonomic homogenization has been documented which can decrease the diversity of biological interactions and reduce resilience to disturbance (Cardoso *et al.*, 2020 ; Piano *et al.*, 2020).

Beyond providing habitat to soil biodiversity in cities, urban soils also provide important contributions to human populations. These contributions include carbon sequestration with soil acting as a carbon sink via soil organic matter (SOM) (Lal *et al.*, 2021 ; O'Riordan *et al.*, 2021b). However the carbon sequestration potential of urban soils is still ambivalent, given that green infrastructures and the energy required for their maintenance can lead to negligible carbon sinks or even a source (O'Riordan *et al.*, 2021a ; Pataki *et al.*, 2021 ; Velasco *et al.*, 2016). Input of carbon to soils comes from different dead organic matter sources, like microbes, plants or dead animals (Chen *et al.*, 2018). Unsealed urban soils can also help to mitigate episodes of heavy rains by minimizing the surface runoff and potentially reducing floods in residential areas which can be a concern in municipalities with a combined rain water and waste water infrastructure (Adhikari et Hartemink, 2016 ; Keeler *et al.*, 2019 ; Lal *et al.*, 2021 ; O'Riordan *et al.*, 2021b ; Roy *et al.*, 2012).

The structural complexity of vegetation in cities offers a gradient of habitats that may also influence the biodiversity of soil organisms like arthropods with previous studies noting an increase in species richness in more complex habitats compared to areas with less vegetation (Beninde *et al.*, 2015 ; Durán et Delgado-Baquerizo, 2020 ; Turrini et Knop, 2015). These urban green infrastructures are supported by unsealed soils organized in a mosaic of vegetation types of varying vegetation complexity and size like municipal parks, residual woodlands or gardens that influence biodiversity and associated ecosystem functions (Ignatieva *et al.*, 2020 ; Roeland *et al.*, 2019 ; Roy *et al.*, 2012). The complexity of this vegetation can be seen in the variety of vertical structures ranging from simplified lawns ecosystems, to lawns with isolated trees or ornamental shrub plantations that can influence arthropod communities by affecting interactions between species and offering different habitats (Francoeur *et al.*, 2021 ; Randlkofer *et al.*, 2010 ; Schuldt *et al.*, 2019). This vegetation may also influence soil properties like the sequestration of carbon aboveground that can be transferred belowground or by the interception of rain that reduces the load that infiltrates the soil (Pataki *et al.*, 2021 ; Phillips *et al.*, 2019b ; Sarah *et al.*, 2015). All these elements show that the surface management in cities is linked to multiple ecosystem functions and has the potential to benefit various life forms.

Our objectives in this study were (1) to assess whether the structural complexity of common types of urban vegetation could affect the diversity of the soil macrofauna community assessed at the taxonomical level of the order and (2) to assess whether vegetation complexity influenced soil properties of interest, more precisely soil organic matter, water infiltration capacity, temperature, compaction and humidity. We hypothesized that the complexity of vegetation, while creating different habitats for the fauna will increase the overall soil macrofauna richness. To answer these questions, four types of green infrastructures prevalent in the city of Montreal, Quebec, Canada were sampled in summer 2020.

1.3 Material and methods

1.3.1 Experimental design and sites

We selected four urban vegetation types (lawns, single trees surrounded by lawn, ornamental shrubs and urban woodlands) representing different types of green infrastructure typically present in the city of Montreal, Quebec, Canada (45° 30′ 31″ N, -73° 33′ 14″ W). Each of these vegetation types was present in three different sites (not always the same ones) and replicated five times within each site to give a total of 60 plots. Because not all sites featured the four vegetation types, a total of five sites which encompassed a variety of contexts were included in the study (Fig. 2, Annexe A). These included two university campuses: the Université du Québec à Montréal (UQAM) campus in the Montreal downtown core and the Loyola campus of Concordia University located in the Côte-des-Neiges-Notre-Dame-de-Grâce borough which is more residential, as well as the emblematic 200 ha Mount-Royal Park, on a Monteregian hill close to the downtown core. These three sites had the three simpler vegetation types that were sampled consisting of lawns dominated by *Poa pratensis* and *Taraxacum officinale*, occurring either without or with urban trees (planted at a density of >5 m distance from one another). All three sites also had ornamental shrub plantations which varied in plant composition. Additionally, within the Mount-Royal Park, we sampled a remnant deciduous woodland dominated by the native *Acer saccharum* and the non-native *Acer platanoides*, that hosts a network of walking trails and receives a high density of visitors. The two other remnant deciduous woodlands dominated by *Acer saccharum* that were sampled included the Bois-de-Saraguay Nature Park and the Bois-de-Liesse Nature Park. The latter two parks are managed extensively with minimal interventions so as to promote the conservation of the initial habitats, but are also well used by the public with a less elaborate network of walking trails. Vegetation was characterized at all sites and an estimate of cover abundance was done using the Braun-Blanquet method (Annexe A). For plots with the presence of a tree, the diameter at breast height (DBH) and the height were measured (Annexe A).

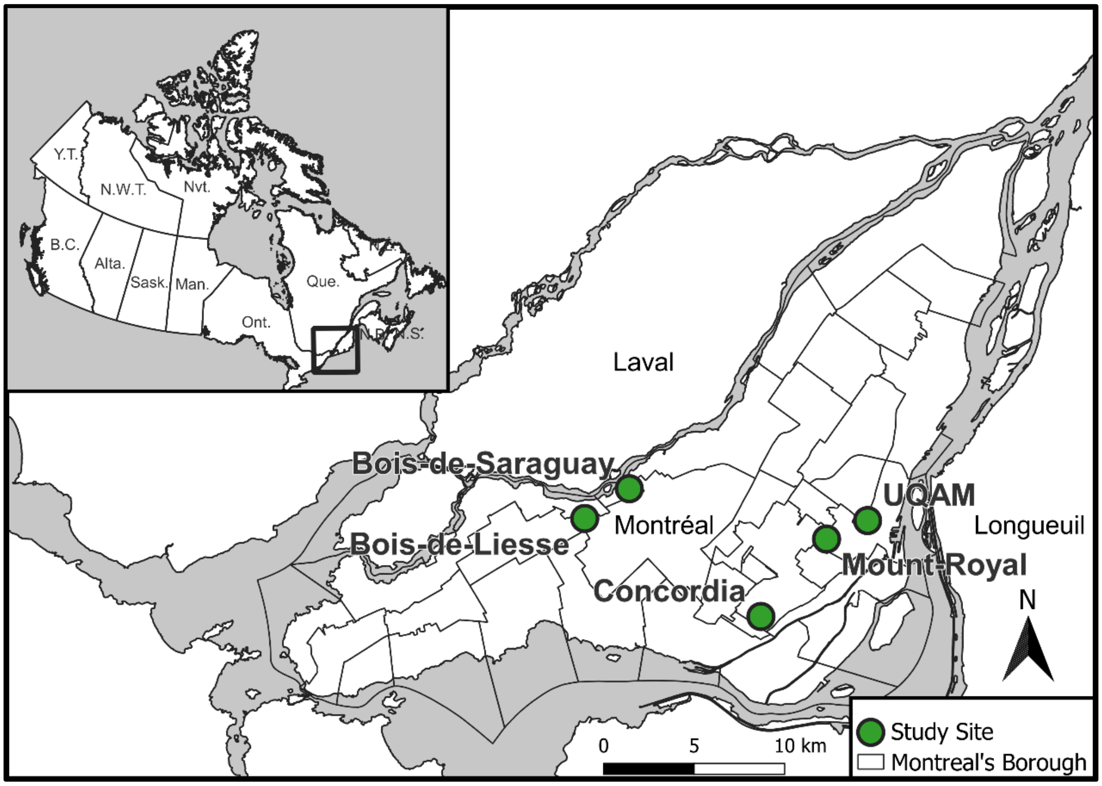

Figure 2 Location of the five study sites in Montreal, Quebec, Canada

1.3.2 Soil macrofauna sampling

Within each site, plots were separated by a minimum of 20 m (50 m in woodlands) to prevent overlap of the invertebrate communities and at least two metres separated the centre of the plot from an impervious surface. All 60 plots were sampled twice in the summer of 2020 (mid-July and late-August). For 2020, the daily mean temperature for the month of July and August was respectively 21.2°C and 20.1°C and the total rainfall was 89.3 mm and 94.1 mm (Environnement Canada, 2023). Soil macroarthropods were assessed with pitfall traps for the duration of 72 hours consisting of a 5 cm diameter plastic cup buried at a depth of 5 cm filled with 50 mL of ethanol of at least 70% and a protective grid top to protect from bycatch but large enough for macroarthropods to fall in (>1 cm). Earthworms were sampled the same day that the pitfall traps were recovered with a mustard extraction technique in every plot with 2 L of a solution of powdered mustard 10 gL^{-1} for 10 minutes on a 20 cm x 20 cm area (Beauséjour *et al.*, 2015). Ten of the 120 traps were compromised because of vandalism or an unforeseen intense rain event (Annexe B). Every macroinvertebrate collected was counted and identified to the order taxonomical rank. Mesofauna taxa like springtails, mites and ticks were excluded from the counting.

1.3.3 Soil measurements

Soil properties were sampled in summer 2020 and 2021. For soil organic matter (SOM) and soil texture, a soil sample of 5 cm depth was collected in the summer 2020 at the same time as the fauna sampling. To determine the amount of SOM, we used the method of loss on ignition at 550°C for six hours with a sample of 15 g (Setälä *et al.*, 2016). Soil texture was obtained with a particle size analysis using the PARIO soil texture analyzer (Meter Environment) in which each soil sample passed through sieves of different diameters and then through the analyzer which calculated the distribution of particles with Stokes's law. The unsaturated soil water infiltration capacity was measured directly in the field using a Mini disk infiltrometer (Meter Environment) where water volume was measured every 30 seconds and at least 20 mL of water flowed during a five minute period. Field measures were adjusted with Van Genuchten parameters and soil texture to determine soil water infiltration rate. Soil humidity was measured via the volumetric water content (VWC) and was taken a total of six times and at least two days following the last rain event with a FieldScout TDR 300 soil moisture meter (Spectrum Technologies) equipped with a 7.6 cm (three inch) rod in both summer of 2020 and 2021. Inside each plot, soil humidity was measured four times in different locations to give an average value. The humidity of all plots was measured once in 2020 on August 27 and five times in 2021 on July 6, July 19, August 17, September 3 and October 1. The average humidity was also measured at the same time as soil water infiltration to assess potential covariance. Soil compaction of the first 10 cm depth was measured on all plot between July 29 and July 30, 2021, with a FieldScout SC 900 soil compaction meter (Spectrum Technologies). The test was done at least 24 hours following any rain event where each measure was taken four times to calculate the mean plot values. Soil temperature was taken for each plot in summer 2021 with HOBO data loggers (Onset Computer Corporation). The data loggers were put in the soil at a depth of 5 cm between July 8 and September 8, 2021, where temperature was registered every hour. The mean temperature for each site during this period was calculated. Unfortunately many data logger were compromised, but at least seven for each vegetation type were retrieved and allowed to compare vegetation types across sites. The means of 52 soil trace elements were determined with a inductively coupled plasma mass spectrometry (ICP-MS) extracted with $CaCl_2$ (0.01 M) to quantify the extractable contents.

1.3.4 Statistical analysis

The linear mixed model of analysis of variance (ANOVA) was used to test whether the abundance of various soil macrofauna orders and soil parameters varied as a function of the fixed variable, vegetation type. Site was included as a random variable. The HSD Tukey was used as a *post hoc* contrast. Assumption (normality and homogeneity of variance) for water infiltration and soil macrofauna orders were not fulfilled, therefore the non-parametric Kruskal-Wallis test with the Dunn test as a *post hoc* contrast was used. Kruskal-Wallis tests did not include site as a random variable. To visualize the association between soil macrofauna and soil properties according to vegetation type, two non-metric multidimensional scaling (NMDS) were performed using the metaMDS() function in the Vegan package (v 2.6-2) (Oksanen *et al.*, 2022). For soil properties, the Bray-Curtis matrix was used and soil temperature was not included for the NMDS and all subsequent tests because only 31 of the 60 plots were available. For soil macrofauna, the Hellinger matrix was used and the order mean abundance was used with the exception of Hymenoptera where a presence-absence was used. Hymenoptera was composed almost entirely of ants where abundance is not suited for analyses (Gotelli *et al.*, 2011). A correlation test was performed on the soil properties using respectively the corr() and corrplot() functions. An absolute value of the correlation level was fixed to 0.50. Since compaction covaried significantly with SOM, it was omitted from linear model tests (Annexe C). To test whether macrofauna order abundance varied as a function of studied factors, a generalized linear mixed model (GLMM) with a poisson distribution was used with vegetation type and soil properties as fixed variables. The vegetation type constrained by sites was included as a random factor. Only recurring orders, those present in at least 10% of the plots, were selected for these tests. Unless otherwise stated, values are reported as means with their standard error and the statistical significance is reported as $p \leq 0.05$. All statistical data analyses were performed with the statistical software R version 4.2.3 (R Core Team, 2023).

1.4 Results

1.4.1 Urban soil community

Across our study, a total of 5075 individuals comprising 20 different taxonomic orders were identified in the pitfall traps (Table 1.1). Order richness did not vary significantly across vegetation types, showing a consistence mean richness of six orders ($p = 0.25$, Fig. 3). Hymenoptera was composed almost exclusively of ants (Family: Formicidae) and was the most abundant order, with 2265 individuals sampled across all vegetation types. Spider abundance (Order: Araneae) differed significantly among vegetation types ($p < 0.001$, Table 1.1), with three to six times higher abundances in lawns without trees compared to the other vegetation types ($p = 0.017$, Table 1.1). Beetles (Coleoptera) represented the second most abundant order and were present in relatively high numbers in each type of vegetation without any significant differences ($p = 0.11$, Table 1.1). Woodlice (Isopoda) were relatively rare, but their abundance differed significantly among vegetation types ($p = 0.015$, Table 1.1), with higher abundances under ornamental shrubs compared to lawns ($p = 0.048$, Table 1.1). Following mustard extraction, a total of 477 earthworms (Order: Opisthopora) were collected and they were more than twice as abundant in residual woodlands compared to all other vegetation types ($p = 0.002$, Table 1.1).

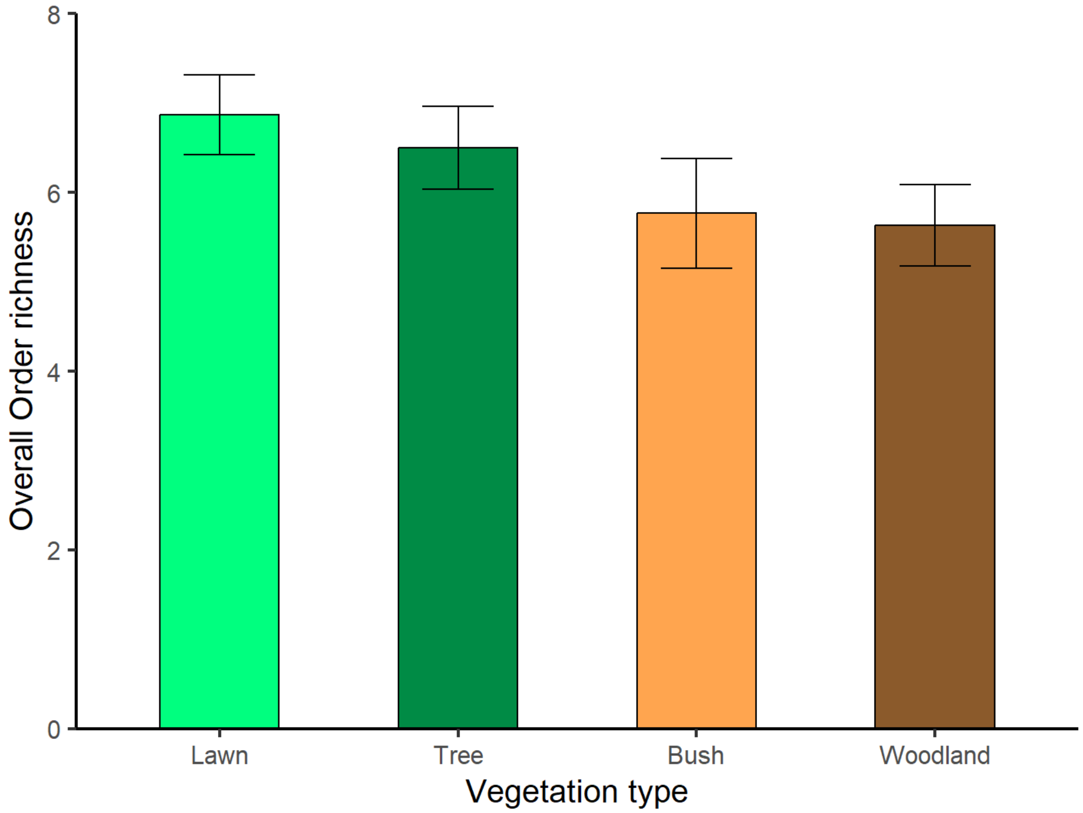

Figure 3 Mean richness (± standard error of the mean) of invertebrates identified to the order present in pitfall traps sampled in lawns (n = 26), under a tree surrounded by lawn (n = 26), under ornamental shrubs (n = 29) or in an urban woodland (n = 29) across sampled sites in Montreal, Quebec, Canada.

Table 1.1 Mean abundance of macroinvertebrate individuals (± standard error of the mean) shown by order that were sampled with pitfall traps and mustard extraction in lawns (n=26 and 30), under a tree surrounded by lawn (n = 26 and 29), under ornamental shrubs (n = 29 and 30) and in urban woodlands (n = 29 and 30) across sampled sites in Montreal, Quebec, Canada. To show the distinction with 0 where no individuals were recorded <1 indicate the presence of an order but with a mean value inferior to 1. Lower case letters below abundance values indicate a significant difference ($p < 0.05$) calculated with the Dunn's test. Hymenoptera are not shown because almost of them where *Formicidae* where the use of abundance is misleading.

Order	**Lawns (n=26 and 30)**	**Trees (n=26 and 30)**	**Bushes (n=29 and 30)**	**Woodlands (n=29 and 30)**
Araneae	6 ± 1.5 a	2 ± 0.6 b	1 ± 0.3 b	1 ± 0.2 b
Archaeognatha	0	0	0	<1
Chordeumatida	0	0	<1	0
Coleoptera	11 ± 2.1	7 ± 1.4	9 ± 2.3	11 ± 2.1
Dermaptera	<1	<1	<1	<1
Embioptera	<1	0	0	0
Hemiptera	2 ± 0.7 a	2 ± 0.6 ab	1 ± 0.3 ab	<1 b
Isopoda	<1 b	<1 b	2 ± 0.7 a	<1 ab
Julida	<1	<1	<1	1 ± 0.1
Lepidoptera	0	0	<1	0
Opiliones	<1	<1	1 ± 0.7	1 ± 0.5
Opisthopora	2 ± 0.6 b	1 ± 0.6 b	4 ± 1.0 b	9 ± 1.4 a
Orthoptera	0	<1	<1	1 ± 0.2
Psocoptera	<1	0	<1	0
Thysanoptera	<1	0	<1	0
Thysanura	0	0	0	<1
Total	44 ± 4.5 a	73 ± 16 a	46 ± 11 ab	20 ± 2.5 b

1.4.2 Soil properties

The amount of SOM in woodland was almost the double compared to the other types of vegetation, but differed significantly between sampled sites with the Mount Royal containing more than twice compared to the UQAM campus ($p < 0.001$, Fig. 4). Soil water infiltration rate was more than twice as high in lawns with or without trees compared to bushes and woodlands ($p < 0.001$, Fig. 4). Soil moisture was higher in lawns without trees and residual woodlands than in lawns with trees ($p < 0.001$, Fig. 4). Subsurface soil temperatures were on average 3 °C cooler in woodlands than on lawns with or without trees ($p < 0.001$, Fig. 4). Lastly, lawns with or without trees were almost twice as compacted as compared to ornamental shrub plantations or residual woodlands ($p < 0.001$, Fig. 4). With the exception of soil humidity, all measured soil properties of residual woodlands were statistically different than lawns without trees, the two extremes of vegetation complexity. However, the opposite was seen, within lawns where the presence of a tree did not affect soil properties except for soil moisture level where average values ranged from 12 to 19 % (Fig. 4)). A correlation was visible between soil compaction and soil water infiltration, where more compacted soil had a higher water infiltration speed (Fig. 4). The visual representation of the soil properties shown by vegetation type indicated that both types of lawn overlapped with each other but that woodlands were different from lawns (Fig. 5). Ornamental shrubs suggested a middleground habitat and overlapped partially with lawns and woodlands (Fig. 5). As for the amount of trace elements in the soil in the different types of vegetation, potassium (K) concentration under ornamental bushes was twice as more abundant than in lawns without trees and residual woodlands ($p = 0.005$, Annexe D) and copper (Cu) concentrations were four times higher in lawns without trees than in residual woodlands ($p = 0.045$, Annexe D). For all other trace elements, no differences were observed.

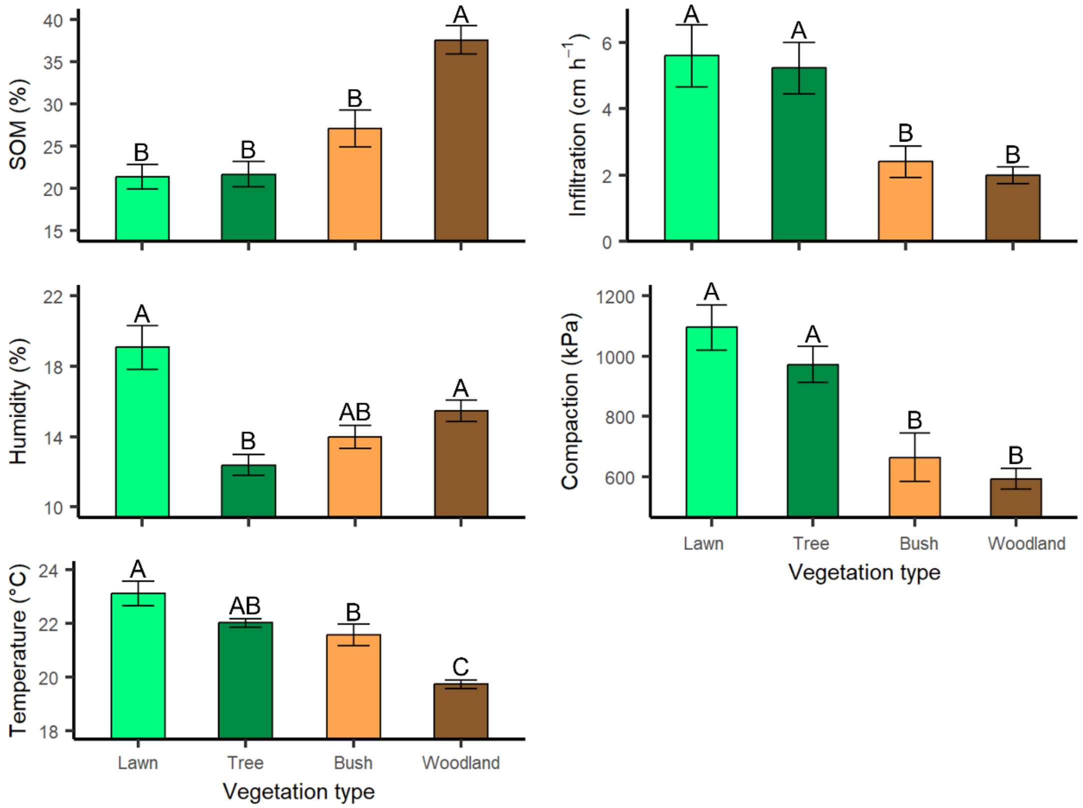

Figure 4 Means (± standard error) of the soil organic matter concentration, soil water infiltration rate, soil humidity, soil compaction and soil temperature across four urban vegetation types in Montreal, Quebec, Canada. Statistically significant differences between vegetation types were tested with the Tukey HSD or Dunn test at the 0.05 level and are shown in uppercase letters.

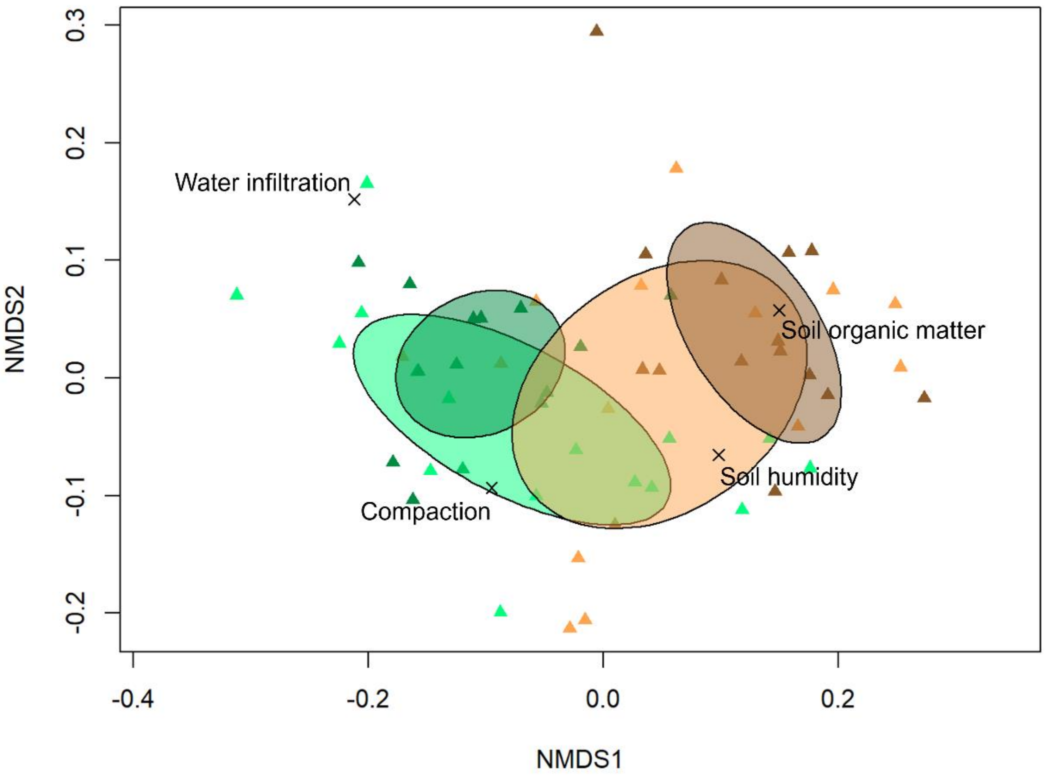

Figure 5 NMDS of the soil properties sampled in lawns (n = 15), single trees surrounded by lawn (n= 14), ornamental shrubs (n = 15) and woodlands (n = 15) in Montreal, Quebec, Canada. The vegetation types are represented as coloured circles (centroids) and triangles (plots) as light green = lawn, dark green = lawn with a single tree, orange = ornamental shrubs and brown = woodland. The stress value of this NMDS is 0.107.

1.4.3 Soil macrofauna composition and soil properties across the type of vegetation

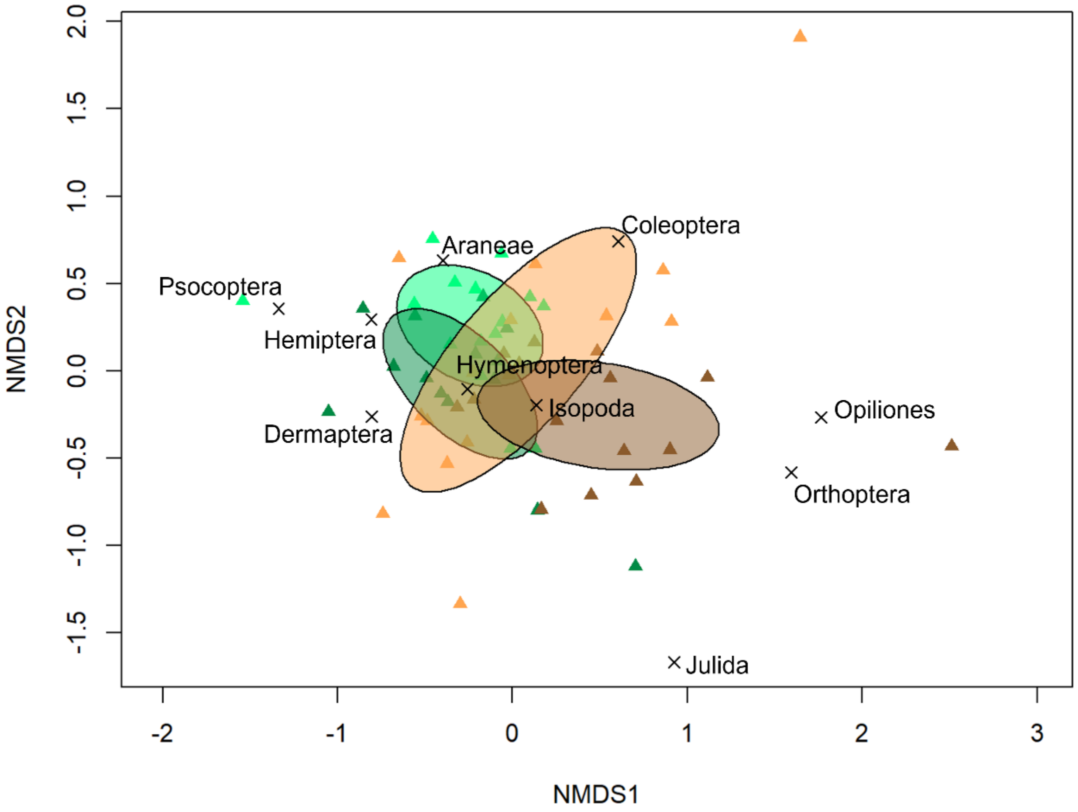

Figure 6 NMDS of the abundance of soil macrofauna orders sampled in pitfall traps in lawns (n = 15, ligh green), single trees surrounded by lawn (n= 14, dark green), ornamental bushes (n = 15, orange) and woodlands (n = 15, brown) in Montreal, Quebec, Canada. The vegetation types are represented as coloured circles (centroids) and triangles (plots). The stress value of this NMDS is 0.194.

The mean abundance of six of the nine recurring orders were significantly associated with at least one of the soil properties (Table 1.2). Soil humidity was the most important predictor, explaining six of the nine orders (Table 1.2). When SOM and soil water infiltration were significant predictors of the mean abundance of a particular taxa, so was soil humidity (Table 1.2). Isopoda was the only taxa where its mean abundance was significant with both the vegetation type and the three tested soil properties (Table 1.2). Araneae abundance was significant with vegetation type and the soil properties, but only marginally significant in the case of SOM (Table 1.2). Julida and Psocoptera were the only recurrent taxa where their abundance were non-significant with both vegetation and any soil properties (Table 1.2). Soil macrofauna order composition varied across the type of vegetation ($p < 0.001$) with woodland being distinct from other vegetation types ($p = 0.047$). The soil macrofauna composition in both types of lawn were not different between each other ($p = 0.085$), but were different when compared to shrubs ($p < 0.05$) (Table 1.3). The visual representation of soil macrofauna order composition across vegetation types (Fig. 6) was similar to the one for the soil properties (Fig. 5).

Table 1.2 Statistical output of the GLMM of mean abundance of macrofauna predicted by vegetation type and soil properties in Montreal, Quebec, Canada. The value shown represents the likelihood ratio Chi-squared test, with the symbol afterward showing the p-value: * = <0.05, ** = <0.01, *** = <0.001.

Orders	**Vegetation**	**SOM**	**Infiltration**	**Humidity**
Araneae	**48.0469*** **	**3.5725.**	**4.7720***	**4.3467***
Coleoptera	4.7439	**14.4957*** **	**22.5390*** **	**17.2656*** **
Dermaptera	2.9908	0.0706	**3.2157.**	**6.4165***
Hemiptera	5.7822	1.8243	0.5640	**15.8213*** **
Isopoda	**8.6431***	**5.8086***	**5.3065***	**6.4327***
Julida	6.0250	1.3602	0.2610	2.4056
Opiliones	**20.4815*** **	0.2800	0.3072	0.2208
Orthoptera	**10.0073***	0.1742	0.5268	**4.5184***
Psocopotera	0.2441	5.2335	1.5601	0.0001

Table 1.3 Statistical output of the PERMANOVA and pairwise test of the soil macrofauna community across the type of vegetation in Montreal, Quebec, Canada. (10000 permutations). Df: Degree of freedom; SS: Sum of squares; F: F value.

Factor	**Df**	**F**	**R^2**	**p**
Vegetation	3	3.902	0.175	<0.001
Lawn x Tree	1	1.546	0.054	0.185
Lawn x Shrub	1	5.239	0.158	<0.001
Lawn x Woodland	1	9.108	0.245	<0.001

Tree x Shrub	1	2.559	0.087	0.018
Tree x Woodland	1	4.768	0.150	<0.001
Shrub x Woodland	1	2.038	0.068	0.047
Residual	55		0.825	

1.5 Discussion

1.5.1 Soil macrofauna communities

Soil macrofauna order richness was not affected by urban vegetation complexity like we expected, but the community composition did vary, mostly between lawns without trees and residual woodlands. Low-level complexity of vegetation, like lawns have been shown to have a more simplified community of soil invertebrates (Kotze *et al.*, 2022 ; Threlfall *et al.*, 2017). Richness patterns are typically assessed at the finer species taxonomical level like species or ecological function and are subsequently incorporated in a broader taxonomical group (Fenoglio *et al.*, 2020 ; Kotze *et al.*, 2022). Thus while taxonomic diversity patterns inside taxa like spiders or ground beetle are documented it is unsurprising that taxa richness did not vary at the order level (Fenoglio *et al.*, 2020 ; Kotze *et al.*, 2022 ; Philpott *et al.*, 2014 ; Piano *et al.*, 2020). The observed variation of soil invertebrate composition as a function of vegetation type could be the result of the variation of the canopy openness between vegetation types. The intensity of disturbance of habitats in urban areas like mowing, litter removal and fragmentation of the landscape could alter ecological interactions such as predation and result in a change to habitat preferences (Faeth *et al.*, 2011 ; Saari *et al.*, 2016). In the case of spiders, while not quantified, most of the sampled individuals were ground-dwelling spiders from the Lycosidae family which actively hunt their prey. The openness of canopy is positively associated with the abundance and activity of this family due to a a higher number of potential herbivores or potential prey (Černecká *et al.*, 2020) but also for ground predatory taxa, in general (Philpott *et al.*, 2014). Also, the fragmentation of the landscape, highly present in urban areas, can increase the diversity of predator communities (Kotze *et al.*, 2022 ; Philpott *et al.*, 2014 ; Siemann, 1998). Native tree density and the quality of understory vegetation may influence species occurrence of Coleoptera in cities (Threlfall *et al.*, 2017). Although in their studies, higher tree density negatively affected the species occurrence of Coleoptera, which is the opposite result than we observed (Fig. 5) (Threlfall *et al.*, 2017). While few studies have assessed the abundance of earthworms inside urban areas, it has been shown that grassy areas close to roads seem to have a lower level of abundance compared to urban forests or parks which support our results (Guilland *et al.*, 2018 ; Smetak *et al.*, 2007 ; Vergnes *et al.*, 2017). There is not a strong general consensus on how earthworm abundance may differ in urban versus rural areas (Guilland *et al.*, 2018 ; Smetak *et al.*, 2007 ; Szlavecz *et al.*, 2006).

1.5.2 Soil properties

With the exception of soil humidity, our hypothesis that soil properties would change following the urban forest complexity was partially correct with strong differences visible between extreme vegetation types (lawns compared to residual woodlands), although some differences, such as with soil water infiltration capacity, were contrary to expectations (Fig. 4). Vegetation type has been shown previously to explain soil properties such as total soil carbon which can be higher in urban areas compared to rural areas or forests (O'Riordan *et al.*, 2021b ; Setälä *et al.*, 2016 ; Ziter and Turner, 2018). Total soil C could be explained by the amount of inorganic carbon in urban areas linked to historical usage of land more notably agricultural or vacant lots which can last decades and impact the structure and services provided by soils (Faeth *et al.*, 2011 ; Ziter *et al.*, 2017 ; Ziter and Turner, 2018). Time since new land use can be a factor affecting the amount of C accumulated in the soil; in temperate climates, older areas (> 60 years) accumulate more C than younger area (~ 20 years) (Kotze *et al.*, 2021 ; Ziter et Turner, 2018). The higher amount of SOM measured in remnant woodlands that we observed compared to simpler green areas (Fig. 4) might also be because of anthropogenic drivers like the removal of tree leaf litter and branches in more simplified green infrastructure types (Kotze *et al.*, 2021). Urban soils are clearly important in terms of total C, but in areas without vegetation, the amount usable by organisms remains unclear (O'Riordan *et al.*, 2021a, 2021b ; Ziter and Turner, 2018). Forests and other complex vegetation types are typically associated with a higher soil water infiltration capacity via their root system and lower soil compaction (Levin and Mehring, 2015 ; Ossola *et al.*, 2015 ; Ziter and Turner, 2018). Less compact soil has typically greater porosity thus increasing the possible paths that water can traverse through the soil (Chen *et al.*, 2014 ; Keeler *et al.*, 2019). Unsaturated soil measurements used in our study may not provide the full picture of soil infiltration since field saturated results can offer different outcomes (Ossola *et al.*, 2015). Still, unsaturated measurements can estimate the capacity of the soil to counter surface runoff on low intensity rainfall events (Phillips *et al.*, 2019b). The positive correlation between water infiltration and soil compaction might be specific to unsaturated hydraulic conductivity. In unsaturated soil, the uptake of water is mainly caused by the contact surface area of small pores, rather than their interior volume where the ratio is greater in compacted soil (Alaoui *et al.*, 2011).

1.5.3 Conclusion

Our study showed that vegetation types in cities can influence the community composition of soil macrofauna orders with greatest differences visible between residual woodlands and lawns. Soil properties also varied between vegetation types and soil humidity particularly influenced many order of the macrofauna communities. Planting or protecting more complex green infrastructures in cities should be seen as an adaptation supporting soil invertebrate diversity and providing important contributions to humans living in cities. It is also important to recognize that even simple vegetation like lawns also support biodiversity as seen with predators, like Araneae (Pataki *et al.*, 2021 ; Philpott *et al.*, 2014). Sharing data on soil biodiversity and their associated contributions, as documented in our study, will hopefully help garner support for necessary changes in our forthcoming urban planning decisions (Derkzen *et al.*, 2017).

CHAPITRE 2

Urban woodlands show a distinct ant community and a higher abundance of earthworms compared to simpler green infrastructures

2.1 Abstract

Ants (Formicidae) and earthworms (Lumbricidae) are soil engineers that shape soil structure by creating galleries and transporting sediment through the soil which could potentially diminish undesired urban events like surface water runoff. The effects of vegetation types on both these taxa are still unclear in urban ecosystems and for earthworms, their exotic status in North America prompts the question as to whether cities facilitate their proliferation. Our study aimed to survey ant and earthworm communities to see if there was a link between community metrics and key soil properties. Four types of vegetation, common in urban areas (lawns with and without a single tree, ornamental shrubs and residual woodlands) in the city of Montreal, Quebec, Canada, were sampled. We captured ants with pitfall traps and earthworms by mustard extraction with individuals identified to the species level. Soils were also sampled to determine the amount of organic matter by loss on ignition. Infiltration capacity was measured with a mini disk infiltrometer which required the measure of the soil textural class. Soil humidity and compaction were measured in the field. Ant community composition differed significantly between woodlands and the other types of vegetation, but soil organic matter content and soil humidity could predict only the presence of two ant species. Earthworms were more abundant in woodlands, but there was no clear effect of their abundance on the measured soil properties. The low quantity of mature earthworms sampled did not allow us to assess community composition dynamics. While ornamental shrubs were believed to be a habitat of intermediate complexity between lawns and woodlands, ant communities were dissimilar to the latter. Ant species present in simpler vegetation types included more generalist species compared to specialist species in woodlands, emphasizing the importance of conserving these areas in the urban landscape to increase overall ant diversity.

2.2 Introduction

The rate of heavy rain is expected to increase in the next decades, which will lead to increased surface runoff (IPCC, 2022), particularly in cities that have a lot of grey infrastructure with impermeable soil surfaces (O'Riordan *et al.*, 2021b). Permeable soils offer a nature-based solution by buffering water flow and reducing surface runoff during heavy rain, with soil compaction and soil organic matter as important factors influencing the efficiency of this contribution (Adhikari et Hartemink, 2016 ; O'Riordan *et al.*, 2021b ; Smith *et al.*, 2021). Green infrastructure in municipalities provide unsealed soils and thus habitat to soil macrofauna, that can further mitigate soil water infiltration by creating tunnels and macropores enabling water to pass and delaying surface runoff (Levin et Mehring, 2015 ; Van Schaik *et al.*, 2014). Favouring vegetation growth may thus be a way to influence urban surface runoff by reducing soil compaction (Levin et Mehring, 2015 ; O'Riordan *et al.*, 2021b). Two ubiquitous taxa of soil macrofauna, both qualified as ecosystem engineers are ants (Formicidae) and earthworms (Lumbricidae) (Schultheiss *et al.*, 2022 ; Tóth *et al.*, 2020). They are labelled as such for their capacity to modify the landscape by bioturbation (Bottinelli *et al.*, 2015 ; Franco *et al.*, 2020). They can shape soil physical properties like compaction, aggregation or resource availability through processes such as the decomposition of dead organic matter and nutrient transport (Bottinelli *et al.*, 2015 ; Kotze *et al.*, 2022 ; Noreika *et al.*, 2015). The main mechanism is by the creation of macropores in the soil via galleries, although the strategy within taxa varies considerably (Bottinelli *et al.*, 2015 ; Franco *et al.*, 2020).

Ants are social insects, with one of the highest abundances worldwide, and show a variety of trophic and nesting strategies and interactions with other organisms (King *et al.*, 2013, 2018 ; Parker et Kronauer, 2021). Urban ant habitat is characterized by a relatively higher temperature and a fragmented vegetation cover of various dimensions compared to more rural or less disturbed areas (Ignatieva *et al.*, 2020 ; Setälä *et al.*, 2016). Ants of urban areas differ from those of forest areas by their behaviour and anatomical features with generalist species being more prevalent (Baudier *et al.*, 2015 ; Clarke *et al.*, 2008 ; Lessard et Buddle, 2005 ; Nielsen *et al.*, 2014). Nesting strategy of urban ants is often seen with the creation of galleries where ants dig deeper in the soil (Andersen, 2019 ; Del Toro *et al.*, 2015), although ant nests are also built in dead or living wood or even inside leaves of living trees (Andersen, 2019 ; King *et al.*, 2018 ; Uno *et al.*, 2010). There is still no consensus about the effect of vegetation structure on ant community composition (Clarke *et al.*, 2008 ; Uno *et al.*, 2010), but ant community structure has been shown to influence the rate of bioturbation (Frouz et Jílková, 2008 ; Taylor *et al.*, 2019).

The prevalence of earthworms in North America is said to be influenced by the proximity to the roads which facilitate its spread (Beauséjour *et al.*, 2015 ; Phillips *et al.*, 2019a ; Sackett *et al.*, 2013). Earthworms are grouped as seven ecological categories, with varying habitat and morphological characteristics of their burrow system that, in turn, influence water infiltration capacity of soils (Blouin *et al.*, 2013 ; Bottinelli et Capowiez, 2021). Earthworm pores created through their galleries help aeration and facilitate the flow of water by reducing compaction (Van Shaick et al. 2014). Many organisms depend on the fragmentation and decomposition of soil organic matter done by earthworms which make different nutrients available at different depths of the soil (Craven *et al.*, 2017 ; Ferlian *et al.*, 2018 ; Tóth *et al.*, 2020). But with most earthworms being exotic and invasive in North America, their presence results in a disadvantage to many native plant and soil fauna species (Craven *et al.*, 2017 ; Ferlian *et al.*, 2018). A survey of urban earthworm species could put light on how much this taxon is present in cities and if their community structure is linked with key soil properties.

The aim of our study was to survey ant and earthworm communities across four common types of urban vegetation representing a complexity gradient (lawns with or without trees, ornamental shrubs and residual woodlands) in Montreal, Québec, Canada. For ants, we sought to evaluate (1) how community structure varied across vegetation types and (2) whether it influenced soil properties such as water infiltration. For earthworms, we assessed (3) how abundant they were across vegetation types and (4) whether their abundance was linked with SOM and water infiltration. We hypothesized that (1) the complexity of vegetation (residual woodlands and trees surrounded by lawns) would provide unique niches for ant and earthworm communities and (2) the creation of macropores in the soil by ants and earthworms would influence soil structure and its properties such as soil organic matter, compaction and infiltration rate. Finally (3) the higher capacity of earthworms to disperse in proximity to roads would be reflected in a lower abundance in residual woodlands.

2.3 Material and methods

2.3.1 Experimental design and sites

We selected four urban vegetation types (lawns, single trees surrounded by lawn, ornamental shrubs and urban woodlands) representing different types of green infrastructure typically present in the city of Montreal, Quebec, Canada (45° 30’ 31” N, -73° 33’ 14” W). Each of these types of vegetation was present in three different sites and replicated five times within each site to give a total of 60 plots. Because the three sites did not all feature woodlands, two additional woodland sites were selected. Therefore, a total of five sites which encompassed a variety of contexts were studied (Fig. 2). These included two university campuses: the Université du Québec à Montréal (UQAM) campus in the Montreal downtown core and the Loyola campus of Concordia University located in the Côte-des-Neiges-Notre-Dame-de-Grâce borough which is more residential, as well as the emblematic Mount-Royal Park. These three sites had simpler types of vegetation with lawns dominated by *Poa pratensis* and *Taraxacum officinale*, occurring either without or with urban trees (planted at a density of >5 m distance from one another). All three sites also had ornamental shrub plantations which varied in plant species composition. Additionally, within the Mount-Royal Park, an area of approximately 200 ha close to the downtown core, remnant deciduous woodlands dominated by *Acer saccharum* and the non-native *Acer platanoides*, that host a network of walking trails, were sampled. The two additional remnant deciduous woodland parks dominated by *Acer saccharum* were the Bois-de-Saraguay Nature Park and the Bois-de-Liesse Nature Park, that are managed extensively by the municipality with minimal intervention. Vegetation cover was identified and an estimate of cover abundance was done using the Braun-Blanquet method. For plots with the presence of a tree, the diameter at breast height (DBH) and the height were measured (see Annexe A: Table S1).

2.3.2 Soil fauna sampling

Within each site, plots were separated by a minimum of 20 m (50 m in woodlands) to minimize overlap of communities and at least two metres separated the centre of the plot from an impervious surface. All 60 plots were sampled twice in the summer of 2020 (mid-July and late-August). For 2020, the daily mean temperature for the month of July and August was respectively 21.2°C and 20.1°C and the total rainfall was 89.3 mm and 94.1 mm (Environnement Canada, 2023). Ants were assessed using pitfall traps consisting of a 7 cm diameter plastic cup buried at a depth of 10 cm filled with 50 mL of ethanol of at least 70% and a protective grid top to protect from bycatch but large enough for macroarthropods to fall in (> 1 cm). Earthworms were sampled on the same day that pitfall traps were recovered with a mustard extraction technique in every plot with 2 L of a solution of powdered mustard 10 g L^{-1} for 10 minutes on a 20 cm x 20 cm area (Beauséjour *et al.*, 2015). Ten of the 120 traps were compromised because of vandalism or an unforeseen intense rain event (Annexe B). Every ant and mature earthworm collected was identified to the species when possible with taxonomical guides (Ellison et al. 2012; Reynolds, 1977). For ants, some species names have been updated since the taxonomical guide publication (Annexe E).

2.3.3 Soil measurements

Soil properties were sampled in summer 2020 and 2021. For organic matter and soil texture, a soil sample of 5 cm depth was collected in the summer 2020 at the same time as fauna sampling. To determine the amount of organic matter, we used the method of loss on ignition at 550°C for six hours with a sample of 15 g (Setälä *et al.*, 2016). Soil texture was obtained with a particle size analysis using the PARIO soil texture analyzer (Meter Environment) in which each soil sample passed through sieves of different diameters and then through the analyzer which calculated the distribution of particles with Stokes's law. The water infiltration capacity of the soil was measured directly in the field using a Mini disk infiltrometer (Meter Environment) with the volume of water measured every 30 seconds and where at least 20 mL of water flowed and five minutes passed. These measures with the Van Genuchten parameters and the soil texture were needed to determine the rate of soil water infiltration. Soil humidity was taken a total of six times and at least two days following the last rain event with a FieldScout TDR 300 soil moisture meter (Spectrum Technologies) equipped with a 7.6 cm (three inch) rod in both summer of 2020 and 2021. Inside each plot, humidity was measured four times in different locations to calculate an average value. The humidity of all plots was measured once in 2020 on August 27 and five times in 2021 on July 6, July 19, August 17, September 3 and October 1. Average humidity was also measured at the same time as soil water infiltration rate to assess possible covariance. Soil compaction to 10 cm depth was measured on all plots between July 29 and July 30, 2021, with a FieldScout SC 900 soil compaction meter (Spectrum Technologies). Measurements were taken at least 24 hours following any rain and the rod and each measure was taken four times to calculate the mean plot value. Soil temperature was taken for each plot in summer 2021 with HOBO data loggers (Onset Computer Corporation). Data loggers were put in the soil at a depth of 5 cm between July 8 and September 8, 2021, and temperature was registered every hour to calculate mean temperature during this period. Unfortunately several data loggers were compromised, but at least seven for each vegetation type were retrieved and allowed to compare vegetation types across, but not within, sites. The mean concentrations of 52 soil trace elements were determined with an inductively coupled plasma mass spectrometry (ICP-MS) extracted with $CaCl_2$ (0.01M) to quantify the extractable contents.

2.3.4 Statistical analysis

The use of presence-absence for ants was used instead of the abundance of individuals. The abundance of ants varies between species and depends on the proximity and density of nests which was not taken into consideration in this study (Gotelli *et al.*, 2011 ; Schlick-Steiner *et al.*, 2006). To visualize the ant communities across vegetation types, a nonmetric multidimensional scaling (NMDS) with the presence/absence of species using the metaMDS() function was done with the Vegan package (v 2.6-2) (Oksanen *et al.*, 2022). We assessed whether ant communities differed between vegetation types with a permutational multivariate analysis of variance (PERMANOVA) with the adonis2() from the Vegan package (v 2.6-2) (Oksanen *et al.*, 2022). *Post hoc* tests were done to determine pairwise contrasts of vegetation types with the pairwise.adonis2() function in the pairwiseAdonis package. A correlation test was performed on the soil properties using respectively the corr() and corrplot() functions with the corrplot package (Taiyun Wei et Viliam Simko, 2021). An absolute value of the correlation level was fixed to 0.50. Since compaction exceeded the threshold and showed strong covariation with SOM, it was omitted from linear model tests to avoid collinearity (Annexe C). To determine how recurring ant species varied by vegetation type and measured soil properties, a generalized linear mixed model (GLMM) with a negative binomial distribution was performed. The presence-absence of an ant species was the response variable while vegetation type and the various soil properties were fixed variables. Furthermore, vegetation constrained by site was included as a random factor. Only species present in at least 10% of the plots were tested. GLMM were done with glmer() from the lme4 package (Bates *et al.*, 2015). For earthworms, only 67 individuals were identified to the species which was not enough to perform a multivariate analysis on community composition. Instead, a Kruskal Wallis test with a Dunn test as a *post hoc* contrast was done to test whether mean abundance of earthworms varied across vegetation types. To see if there was a relation between earthworm abundance and soil properties (SOM and soil infiltration), a linear regression was calculated with earthworm abundance as the explanatory variable and the soil properties as the dependant variable.

Unless otherwise stated, values were reported as means with their standard error and the statistical significance was reported as $P \leq 0.05$. All statistical data analyses were done using the statistical software R version 4.2.3 (R Core Team, 2023).

2.4 Results

2.4.1 Ant communities

Across the study, 2938 individuals comprising 39 species or morpho-species from 16 genera were identified (Table 2.1). Six morpho-species were designated only to the genus level when species could not be clearly confirmed. Species were almost exclusively from the Formicinae and the Myrmicinae subfamilies, with the exception of the Dolichoderinae represented by a species of the *Tapinoma* genus. *Lasius* was the most common genus present in every vegetation type followed by *Formica* although the latter was almost absent in woodlands. Total ant species richness was higher in the simplest vegetation type in lawns without a tree with a richness of 25 species, close to the double than residual woodland with 14 species (Table 2.1). Total ant species richness in lawns with trees and ornamental bushes were intermediate with respectively 22 and 18 species (Table 2.1). A total of 12 species or morpho-species within eight genera were recurrent and present in at least 10 % of the plots. *Lasius neoniger* was the most encountered species, present in two thirds of the plots. Some recurrent species were not present in all vegetation types, with many being totally absent in woodlands like *Brachymyrmex depilis*, *Formica subaenescens, Temnothorax schaumiii* and *Tetramorium immigrans*. The only recurring species showing an opposite trend was *Aphaenogaster picea*. *Lasius americanus* showed a unique pattern with complete absence under ornamental shrubs, but presence in the three other vegetation types, with a preference for woodlands (Fig. 7). This habitat preference contrasted to congeneric species *Lasius neoniger*, that was almost absent in woodlands (Table 2.1, Fig. 7). *Myrmica incompleta* showed a trend similar to *Lasius americanus*, but was present in the four types of vegetation while still having a preference for woodlands (Table 2.1, Fig. 7).

Table 2.1 Occurrence of ant species present in pitfall traps sampled in lawns (n = 15), under a tree surrounded by lawn (n = 14), under ornamental shrubs (n = 15) and in urban woodlands (n = 15) across sampled sites in Montreal, Quebec, Canada. Species of ants present in at least 10 % of the plots are considered recurrent and written in bold. cf. refers to individuals uncertain to be a distinct species but are alike to a known species and spp. refers to species identified only to the genus level.

Species	**Lawns (n = 15)**	**Trees (n = 14)**	**Shrubs (n = 15)**	**Woodlands (n = 15)**
Aphaenogaster fulva	0	0	0	1
Aphaenogaster picea	0	0	0	6
Brachymyrmex depilis	2	2	5	0
Camponotus herculeanus	0	0	0	2
Camponotus pennsylvanicus	0	1	0	0
Crematogaster spp.	0	1	0	0
Formica argentea	1	1	1	0
Formica dolosa	0	0	1	0
Formica incerta	1	0	0	0
Formica lasioides	2	3	0	0
Formica neogagates	1	3	1	1
Formica sp.	1	0	0	0
Formica subaenescens	4	2	4	0
Lasius americanus	4	4	0	7
Lasius cf. niger	1	0	0	0
Lasius neoniger	13	12	13	1
Lasius pallitarsis	1	1	0	0
Lasius speculiventis	1	1	0	0
Lasius spp.	0	3	2	1
Lasius subglaber	0	1	2	0
Lasius umbratus	0	3	0	0
Monomorium florican	1	0	0	0
Myrmecina americana	1	0	0	0
Myrmica brevispinosa	1	0	0	0
Myrmica incompleta	2	1	1	5
Myrmica rubra	3	1	1	3

Nylanderia parvula	0	1	1	0
Prenolepis impairs	1	0	0	0
Solenopsis cf. texana	4	1	4	0
Solenopsis molesta	2	1	2	0
Stenamma brevicorne	0	0	0	2
Stenamma impar	0	0	0	1
Tapinoma sp.	1	0	0	0
Temnothorax americanus	2	0	1	0
Temnothorax curvispinosus	0	0	2	2
Temnothorax longispinosus	0	0	0	1
Temnothorax schaumiii	4	1	2	0
Temnothorax texanus	1	2	1	1
Tetramorium immigrans	2	2	4	0
Number of species found	25	22	18	14

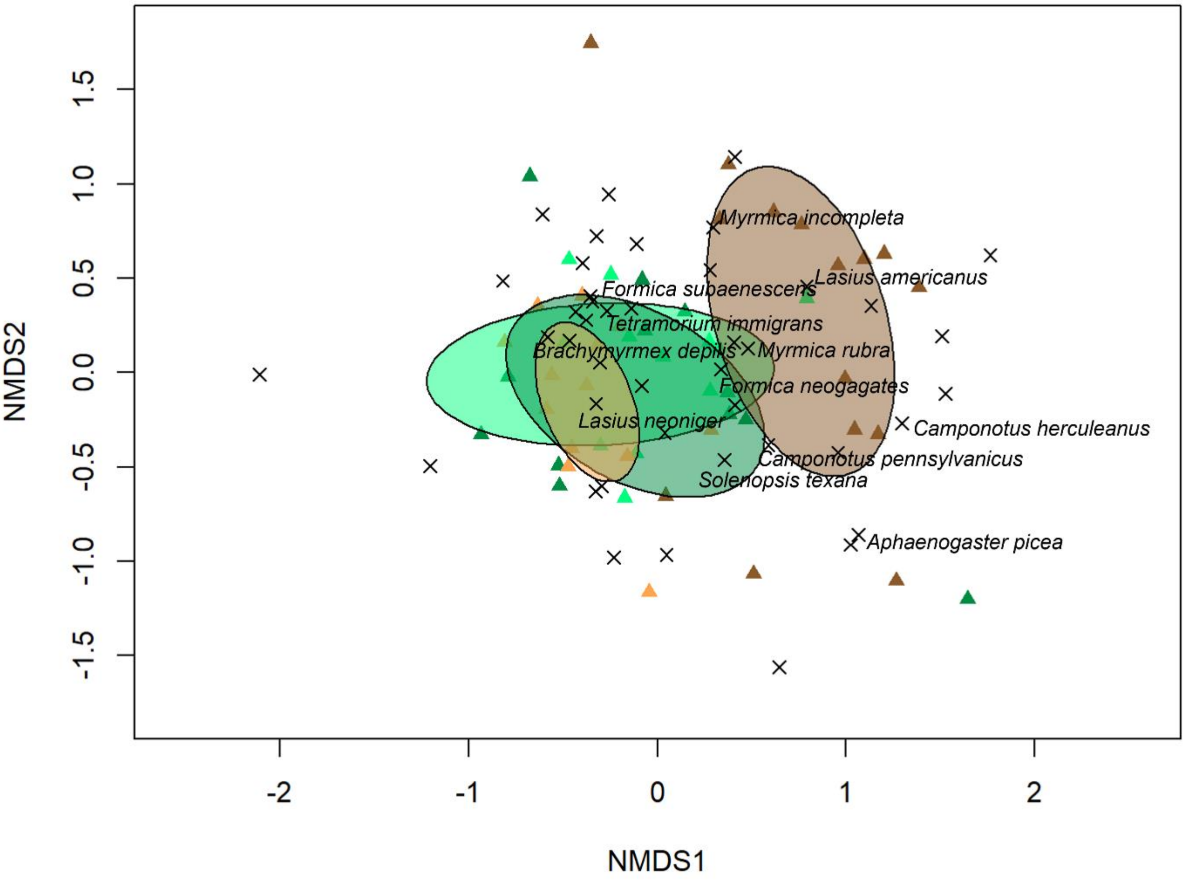

Figure 7 NMDS of the presence of ants species sampled by pitfall traps in lawns (n = 15), single trees surrounded by lawn (n= 14), ornamental bushes (n = 15) and woodlands (n = 15) in Montreal, Quebec, Canada. The types of vegetation are represented as coloured circles (centroids) and triangle (plots) as light green = lawn, dark green = single tree, orange = ornamental bush and brown = woodland. Each ant species are represented as a cross with the name presented only to recurrent species. The stress value of the test is 0.139.

2.4.2 Urban ant communities and their relation to soil

Ant communities showed a distinct species composition in woodlands in contrast to all other vegetation types (F = 4.288, p < 0.001, Table 2.3). Ant communities in both types of lawn and under ornamental shrubs were similar in composition, although under ornamental shrubs showed a smaller breadth (p > 0.1, Table 2.3, Fig. 7). When exploring how vegetation type predicted the occurrence at the species level with a GLMM approach, *Lasius neoniger* was the only recurrent ant species that differed significantly (Table 2.2, p = 0.047), reflecting its near absence in woodlands (Table 2.1). Soil properties were not strong predictors for the presence of recurring ant species (Table 2.2). Soil organic matter concentration marginally predicted the occurrence of *Lasius neoniger* (p = 0.057, F = 3.625, Table 2.3) and *Solenopsis cf. texana* (p =

0.058, F = 3.602, Table 2.3). Soil humidity marginally predicted the occurrence of with *Lasius neoniger* (p = 0.067, F = 3.362, Table 2.3).

Table 2.2 Statistical output of the GLMM of ant species occurrence measured against vegetation type and three measured soil properties in Montreal, Quebec, Canada. The value shown represents the likelihood ratio Chi-squared test, with the symbol afterward showing the p-value: . = p <0.1,* = p <0.05. Note: *Aphaenogaster picea* was tested using a LMM because an output with a GLMM was not possible.

Ant species	**Vegetation**	**SOM**	**Infiltration**	**Humidity**
Aphaenogaster picea	1.8997	2.1231	0.1866	0.0182
Brachymyrmex depilis	2.9379	0.4517	0.1676	2.1772
Formica neogagates	2.1912	0.0081	0.6931	0.0043
Formica subaenescens	0.6953	0.2954	2.1329	0.7753
Lasius americanus	2.4400	0.6921	0.9847	1.5792
Lasius neoniger	**7.9714***	**3.6245.**	0.6045	**3.3621.**
Myrmica incompleta	3.2239	0.0027	0.9220	0.7098
Myrmica rubra	1.1261	0.0498	0.1410	0.6707
Solenopsis cf. texana	2.4986	**3.6023.**	0.1029	0.1471
Temnothorax schaumiii	1.6633	0.1098	0.0234	0.1226
Tetramorium immigrans	0.8824	0.6043	1.5180	2.5806

Table 2.3 Statistical output of the PERMANOVA and pairwise contrasts of ant species community composition across four vegetation types in Montreal, Quebec, Canada. 10000 permutations. Df: Degrees of freedom;; F: F value.

Factor	**Df**	**F**	**R^2**	**p**
Vegetation	3	4.288	0.192	<0.001
Lawn x Tree	1	0.690	0.025	0.735
Lawn x Shrub	1	0.950	0.034	0.494
Lawn x Woodland	1	7.148	0.203	<0.001
Tree x Shrub	1	1.723	0.062	0.114
Tree x Woodland	1	6.329	0.190	<0.001
Shrub x Woodland	1	10.12	0.273	<0.001
Residual	54		0.808	

2.4.3 Earthworm abundance and relation with soil properties

A total of 475 individual earthworms were sampled comprising a total 13 species ranging in density from 0 to 120 individuals m^{-2}. Given a high number of juveniles, only 67 individuals were successfully identified to the genus level with *Lumbricus* representing more than half of the genera, and with 59 individuals identified to the species. *Lumbricus terrestris* was the most common species with a total of 26 individuals. Both lawn vegetation types had the lowest abundances, with respectively on average, 8 ± 2.5 and 6 ± 2.2 earthworms m^{-2}. Although soil under ornamental bushes had, on average, higher densities with 14 ± 3.8 earthworms m^{-2}, they did not differ significantly from either lawn types. In contrast, woodland soils had more than double to quadruple earthworm densities with 35 ± 5.5 earthworms m^{-2} and differed significantly when compared to other vegetation types ($p < 0.001$). It should be noted that 50 of the 119 plots across all types of vegetation did not have any earthworms.

The abundance of earthworms in our study had a significant, but weak positive relation with SOM concentration (Fig. 8, $R^2 = 0.18$). In contrast, the significant relation between earthworm abundance and soil water infiltration rate capacity was a negative one, but very weak (Fig. 9, $R^2 = 0.09$). Our capacity to test these relations was limited given that more than half of our sampled plots had no earthworms at all and more plots with earthworms were in the woodlands.

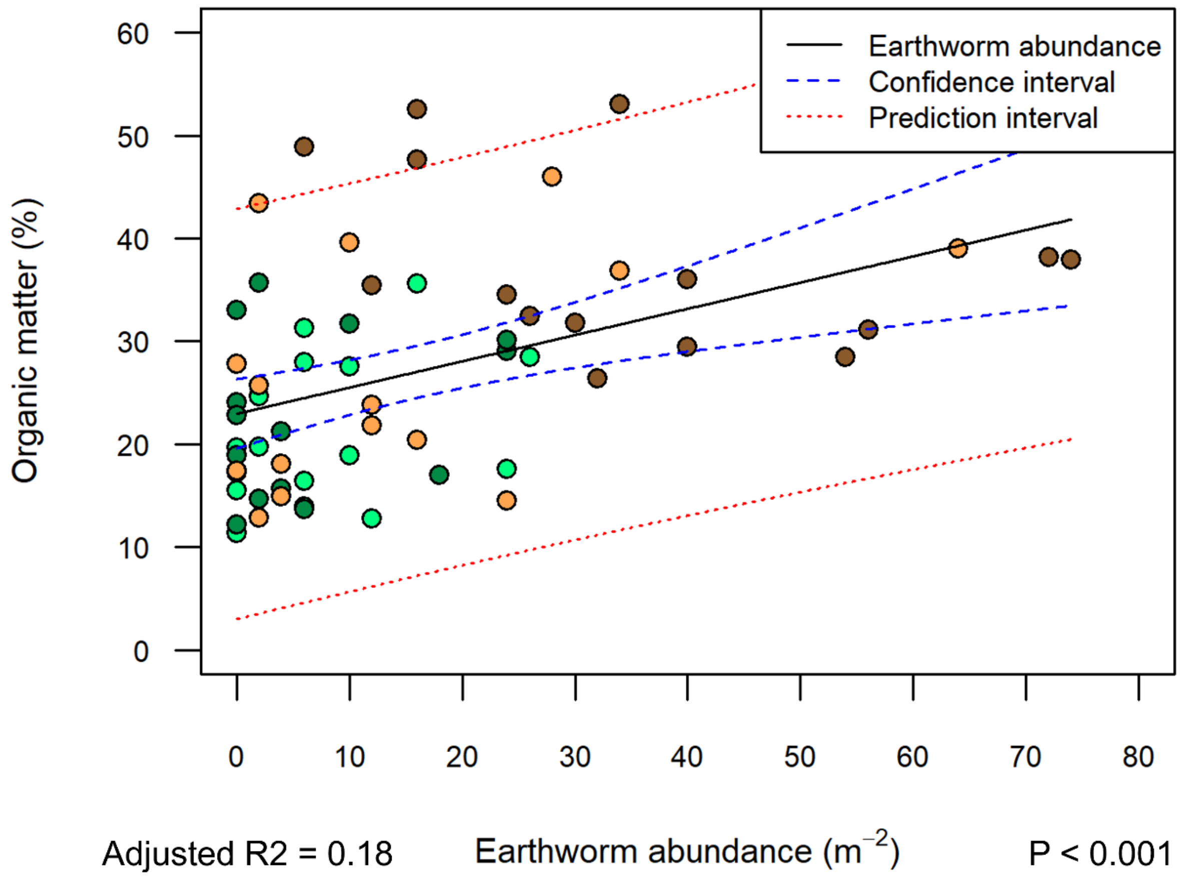

Figure 8 Linear regression models testing the abundance of earthworms as a predictor of soil organic matter with the abundance of earthworms across all samples sites in Montreal, Quebec, Canada. The dots represent the abundance of earthworms. The blue and red dotted lines represent respectively the confidence interval and prediction interval.

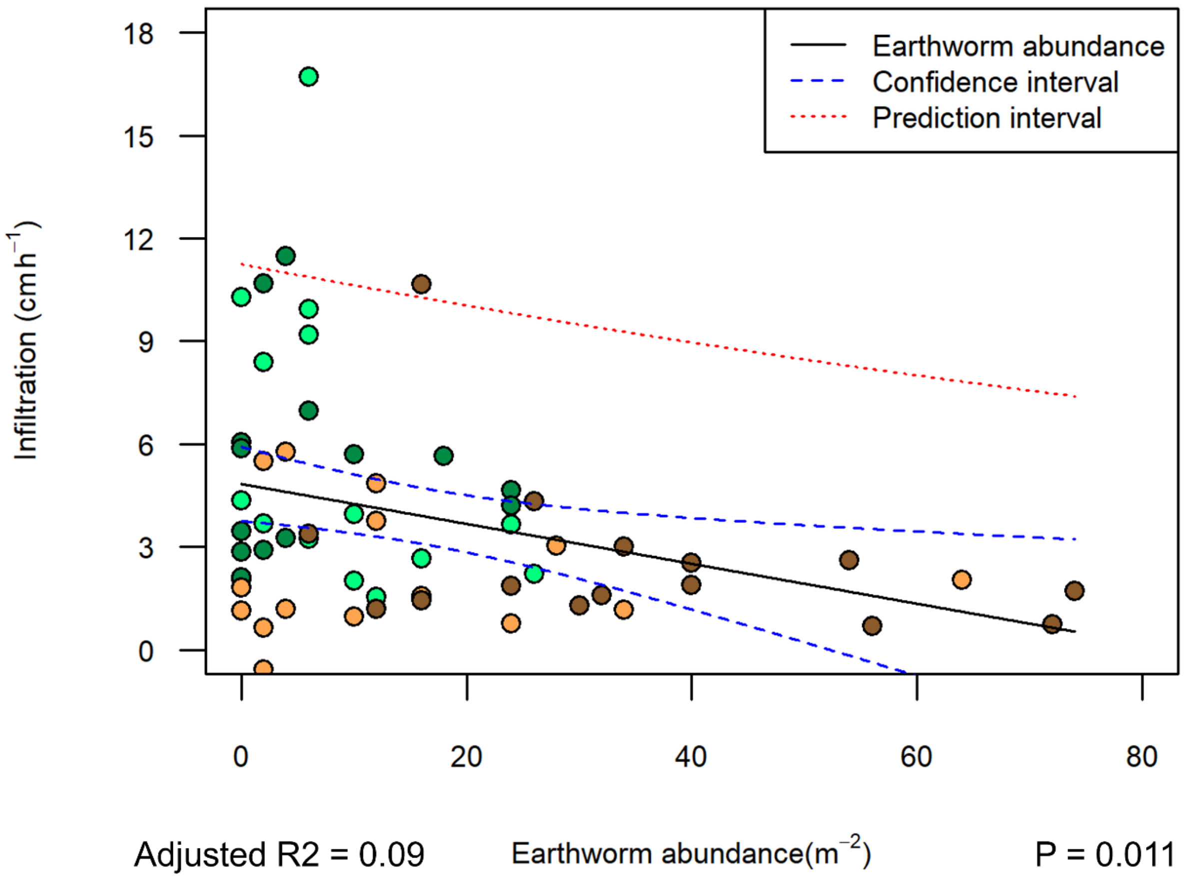

Figure 9 Linear regression between soil water infiltration rate in relation to earthworm abundance across all sample sites in Montreal, Quebec, Canada. The dots represent the earthworm abundance values, while the blue and red doted lines represent respectively the confidence interval and prediction interval.

2.5 Discussion

2.5.1 Ant communities

Ant species community composition in woodlands was different than that in simpler vegetation types (Table 2.3, p < 0.001), but no compositional differences were observed between lawns and ornamental shrubs (Table 2.3, p = 0.114). Among the recurring ant species, only *Aphaenogaster picea* was exclusively present in woodlands (Table 2.1). If we consider rarer ant species, *Aphaenogaster fulva*, *Camponotus herculeanus,* two species of *Stenamma* and *Temnothorax longispinosus* were also present exclusively in woodlands (Table 2.1). These species share a link with trees with both *Aphaenogaster* species and *Camponotus herculeanus* mostly nesting in rotten trees, while *Temnothorax longispinosus* can live under bark of living trees and *Stenamma* species from north-eastern America live typically in or on the edge of forests (Ellison *et al.*, 2012). The presence of the recurring ant species *Brachymyrmex depilis*, *Formica subaenescens and Temnothorax schaumiii* in the simpler types of vegetation (lawns and shrubs), but entirely or almost absent in woodlands was surprising given that they are mostly associated with woods, and not open habitats like lawns (Ellison *et al.*, 2012).The absence of species in woodlands was even more apparent when rarer species were considered. However, the total number of species sampled was higher in simpler vegetation types and decreased as the complexity of vegetation increased (Table 2.1). Woodlands differed from simpler vegetation types by canopy cover characteristics and the presence of woody material on the soil, although all vegetation types provided some canopy cover, and lawns with trees and ornamental shrubs provided some, though limited, access to woody resources. Ants dwelling in habitats with a more open canopy are often generalists and thermophiles, in contrast to ants living in woodlands (Andersen, 2019) which was partially observed in our study with species like *L. neoniger* and *T. immigrans*. Although several studies have indicated that forests have higher soil humidity that can be detrimental to ant presence because of lower nest densities and a increase risk of fungal infection (Clarke *et al.*, 2008 ; Ješovnik et Bujan, 2021), our study showed no difference in soil humidity between extreme vegetation types (Fig. 4). Perhaps these latter conditions do not apply as severely in urban habitats . In short, our hypothesis that ant communities would vary across vegetation types, mostly between extremes, was partially correct.

Unlike the community structure of soil macrofauna orders, where shrubs offered a habitat with the largest breadth of orders, overlapping both lawns and woodland dwelling organisms (Fig. 6), ant communities under urban shrubs showed a narrower breadth to communities inside both lawn types (Fig. 7). The pattern of shrubs offering an intermediate habitat was also observed for Collembola species sampled on the same plots, with the exception that community breadth under shrubs was similar to that observed in lawn habitats (St-Pierre, unpublished data). A characteristic shared with lawn and shrub vegetation types in our study was the particularity of a low quantity of woody material on the soil surface. Dead wood is important for many forest ant species for their nesting ecology (King *et al.*, 2018). The absence of dead woody material could be the result of city management for aesthetic and safety reasons (Carpaneto *et al.*, 2010 ; Lindenmayer *et al.*, 2014). When there was woody materials, it was mostly in the form of small branches or mulch, unlike in residual woodlands where logs or trunks were present. The diameter of the woody material is important for it to be suitable as a nest for ant species, minimally 10 cm diameter for the majority of ants from cool temperate forests (King *et al.*, 2018). The absence of big woody materials in bushes may prevent the colonization of ant species which require woody materials. Otherwise, shrubs are often used along walking paths and thus despite the minimum distance of two meters, many shrub plots were close to impervious surfaces. Impervious surfaces, like pavement, could hinder the presence of ant species that are not thermophilic, but favour others like *Tetramorium immigrans* nicknamed the pavement ant which was more abundant under shrubs compared to t other vegetation types (Ellison *et al.*, 2012).

Soil properties were generally not a good predictor of ant community structure. None of the recurrent species were strongly linked to SOM, soil humidity, soil water infiltration rate or soil compaction. The rare cases were predicting the occurrence of *Solenopsis cf. texana* with SOM concentration and predicting the occurrence of *Lasius neoniger* with both SOM and soil humidity. *Solenopsis* species of the north-eastern America are mostly opportunist ants that can live inside other species nests while *L. neoniger* are ubiquitous in open habitats (Ellison *et al.*, 2012). While ant nests in the soil modify soil structure and SOM in proximity (< 1 m), this effect could not be assessed in our study where nest density and proximity were not evaluated (Cammeraat *et al.*, 2002 ; Cammeraat et Risch, 2008). Although we could not formally test whether soil temperature could predict the presence of recurring ant species given the high number of compromised data loggers, soil temperature decreased as vegetation complexity increased (Annexe D). A lower temperature in woodlands compared to simpler vegetation present in more urbanized areas was not surprising (Clarke *et al.*, 2008 ; Grimm *et al.*, 2008). The high percentage and proximity of impervious areas around plots of lawns and shrubs may have permitted some species more adapted to warmer and drier conditions to live in cooler areas thanks to the heat-island effect (Cordonnier *et al.*, 2020 ; Menke *et al.*, 2011). Cordonnier *et al.*, (2020) offered this explanation for the occurrence of *Tetramorium immigrans*, which we also documented here, as a mechanism for occurring past the northern limit of their range. Still, this explanation should be taken with precaution as the response of a species as a function of latitude and urbanization is strongly variable, even between closely related species (Gippet *et al.*, 2017). Therefore, our hypothesis that soil properties could be as important as vegetation type to explain ant community structure was false.

2.5.2 Earthworm communities

Our study offered some support for the hypothesis that earthworm abundance could predict urban soil properties, but patterns were overall weak and earthworm abundances were low (Fig. 9 – 10). The positive correlation between earthworm abundance and soil organic matter concentration that we observed is in contradiction with Sackett *et al.* (2013) who reported that a high biomass of anecic earthworms was associated with a lower carbon pool. In our case, although most individuals could not be identified to species due to the presence of many juveniles, *Lumbricus terrestris* was the most common earthworm and is often considered an anecic species that creates vertical burrows that can increase drainage and thus water infiltration (Blouin *et al.*, 2013 ; Bottinelli *et al.*, 2020). Our last hypothesis about earthworms being less abundant in residual woodlands because of the proximity to roads also was not supported. *Lumbricus terrestris*, our most encountered species, was less abundant in sites with less leaf litter on the soil, yet highly abundant in residual woodlands. This result challenges previous results suggesting that the proximity and time since anthropological disturbance, mostly close to simpler vegetation, would facilitate the distribution of exotic earthworms (Beauséjour *et al.*, 2015). Also, we believed that the irregularly high temperatures when some of the mustard extractions were done in lawns and under shrubs during the month of July 2020, could have underestimated the abundance sampled since earthworms go deeper in the soil and are less active at higher temperature (Eggleton *et al.*, 2009). The less compacted soil of woodlands compared to lawns could have facilitated the creation of macropores by earthworms and therefore also facilitated colonization (Capowiez *et al.*, 2009 ; Schittko *et al.*, 2022).

2.5.3 Conclusion

In summary, the community structure of ants in woodlands was significantly different than in simpler vegetation types. Ants present in simpler vegetation included more generalist species. The role of shrubs differed between ants and overall soil macroinvertebrate orders, where contrary to the latter, no intermediate habitat quality was detected. Vegetation type was better at explaining ant community structure than measured soil parameters. As for earthworms, woodlands represented a habitat where they seemed to thrive and the aspect of proximity to impervious surface was not a relevant predictor of their abundance. This study put forward the importance of residual woodlands in cities for biodiversity conservation since it they provide refuge to many specialist species that do not occur in simpler vegetation types such as lawns or under ornamental shrubs.

CONCLUSION GÉNÉRALE

Ce mémoire a permis le recensement de plusieurs taxons de la macrofaune invertébrée du sol et particulièrement d'une liste des espèces de fourmis présentes dans différentes types de végétation de la Ville de Montréal. L'importance des boisés résiduels urbains quant à la conservation de la biodiversité est mise de l'avant suite aux variations drastiques des communautés des invertébrés du sol dans les boisés comparées aux types de végétation plus simples où plusieurs espèces de fourmis étaient exclusivement présent dans les boisés. Cependant, cela n'exclut pas le rôle de la végétation plus simple avec les pelouses et arbustes où des fourmis, mais aussi d'autres taxons y montrait des préférences. Quant à la question sur la limitation de l'identification des invertérbrés à l'ordre, elle nécessite beaucoup moins d'expérience que des niveaux taxonomiques plus précis, mais plus de différences seraient perceptibles à un niveau plus précis. Des plateformes de suivi de la biodiversité comme QUBS (https://www.qubs.fr/) possèdent une clé d'identification de la faune du sol avec une précision tentant d'aller jusqu'à l'espèce lorsque possible tout en restant accessible. Ce type de plateforme permet un suivi de la biodiversité avec les aspects positifs attribué à la science citoyenne comme étant éducative et participative du grand public (Bonney *et al.*, 2016).

Quelques pistes pour pousser davantage notre compréhension de la biodiversité de la macrofaune du sol dans la végétation urbaine serait l'utilisation d'un niveau taxonomique plus fine pour d'autres taxons et d'accentuer l'effort d'échantillonnage. La facilité et l'accessibilité à des données taxonomiques peuvent être conservées tout en utilisant un niveau taxonomique comme la famille ou sous-famille. La période d'échantillonnage pourrait être élargie en débutant au mois du mai et s'étaler jusqu'au mois d'octobre pour permettre la présence variable de taxons en raison de leur cycle de vie. Toujours en se limitant à Montréal, le choix des sites pourrait être sélectionné en prenant en compte la gestion de la végétation telle que la fréquence de tonte et l'historique des lieux qui est potentiellement important pour les propriétés du sol (J. St-Pierre, communication personnelle). Une augmentation du nombre de sites permettrait des habitats supplémentaires comme d'autres parcs de taille variable ou des cours de terrains privés.

Améliorer la qualité de vie dans les villes et conserver la biodiversité terrestre sont deux grands objectifs de développement durable et les actions d'un peuvent influencer l'autre (UN, 2021). La Ville de Montréal commence à prendre des actions concrètes pour favoriser la biodiversité urbaine en conservant des troncs ou des branches supérieures à 30 cm dans certains quartiers, tout en partageant les bienfaits reliés (Montréal, 2024). Le bois mort représente un habitat important et influence la biodiversité d'invertébrés qui en dépend dans leur cycle de vie (King *et al.*, 2018, Kotze et al. 2022). Les forêts, urbaines ou non, possèdent une quantité importante de bois morts, mais leur présence dans les aménagements urbains de végétation simple comme les pelouses et les arbustes étaient quasi inexistants. Le changement de pratique de bois permettrait aussi d'incorporer un volet éducatif sur le sujet par exemple via des affiches explicatives (Thorn *et al.*, 2020) de s'y établir.

Notre étude nous amène aussi à suggérer que accroitre la surface occupée par la végétation arbustive sera un autre geste concret favorable pour la biodiversité urbaine. Actuellement, les aménagements arbustifs sont souvent faits sous forme d'ilot de petite surface avec peu de mélange d'espèces. Ainsi, une augmentation de la superficie continue des aménagements arbustifs avec une diversité d'espèces d'arbustes pourrait accroitre leur influence sur la vie dans le sol. En somme, le choix et la gestion de la végétation en zone urbaine a non seulement des impacts esthétiques, mais aussi sur la biodiversité des sols. Ainsi, les résultats et recommandations qui découlent de ce mémoire mettent de l'avant l'importance de considérer le sol vivant également dans les décisions présentes et futures du paysage urbain.

ANNEXE A

Geoprahical and vegetation information regarding the sites used in Montreal, Quebec, Canada. Co-produced with St-Pierre, J.

Table S1. Localization, number of plots and dominant vegetation of the sites used in Montreal, Quebec, Canada.

Type of vegetation	**Université du Québec à Montréal (UQAM)**	**Loyola Campus, Concordia University**	**Mount Royal Park**	**Bois-de-Liesse Nature Park**	**Bois-de-Saraguay Nature Park**
Coordinates	45° 30’ 33”N -73° 34’ 7”W	45° 27’ 29”N -73° 38’ 21”W	45° 30’ 19”N -73° 35’ 16”W	45° 29’ 59”N -73° 46’ 06”W	45° 31’ 02”N -73° 44’ 23”W
Number of plots	15	15	20	5	5
Number of lawn plots	5	5	5		
Number of tree surrounded by lawn plots	5	5	5		
Number of ornamental shrub plots	5	5	5		
Number of woodland plots			5	5	5
Dominant grasses	*Poa pratensis (9)*	*Poa pratensis (13)*	*Poa pratensis (10)*		
Dominant herbaceous species	*Taraxacum officinale (7)* *Plantago major (4)* *Trifolium repens (4)*	*Taraxacum officinale (6)* *Trifolium repens (3)*	*Plantago major (6)* *Taraxacum officinale (6)*		
Dominant shrub species	*Taxus canadensis (2)*	*Rosa rugosa (2)*	*Rubus odoratus (2)* *Diervilla lonicera (2)*	*Rhamus cathartica (2)*	
Dominant seedling species			*Acer saccharum (3)*	*Acer saccharum (3)*	*Acer saccharum (4)*
Dominant sapling species				*Fraxinus pennsylvanica (2)*	*Fraxinus pennsylvanica (3)*
Dominant tree species	*Magnolia acuminata (3)*	*Acer saccharum (2)*	*Acer saccharum (6)*		*Acer saccharum (4)*

	Ginkgo biloba (2)	*Gleditsia tricanthos (2)*			
Mean tree height (m) (± standard error)	7.1 ± 1.2	11.6 ± 1.3	14.1 ± 1.6	17.3 ± 2.8	19.7 ± 1.7
Mean tree DBH (cm) (± standard error)	10.9 ± 1.5	25.8 ± 3.9	21.0 ± 2.1	21.5 ± 3.3	16.2 ± 1.0

ANNEXE B

Details on the uncomprimised pitfall traps

Table S2. Quantity of pitfall traps analyzed for each vegetation type and sites and in total.

Vegetation **Site**	**Lawn**	**Tree surrounded by lawn**	**Ornamental shrub**	**Urban woodland**	**Total**
UQAM	8	9	9	NA	26/30
Concordia	8	10	10	NA	28/30
Mount-Royal	10	7	10	10	37/40
Bois-de-Saraguay	NA	NA	NA	9	9/10
Bois-de-Liesse	NA	NA	NA	10	10/10
Total	26/30	26/30	29/30	29/30	110/120

Each vegetation type within locations had 10 pitfall traps installed. Some pitfall traps were excluded because of vandalism or an intense rain event which flooded the content of the trap or the trap itself from the pit.

ANNEXE C

Correlation test between soil property variables (SOM, water infiltration, compaction and humidity) for the suitability of the linear mixed model

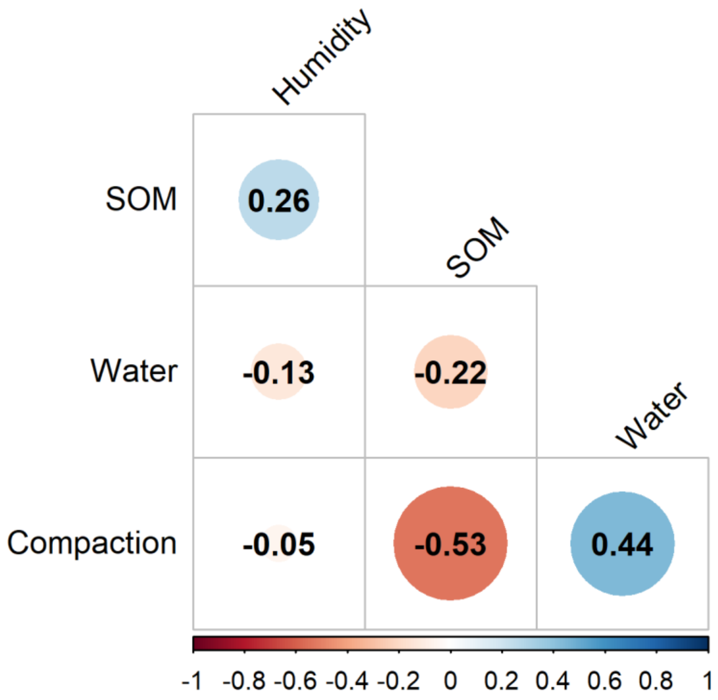

Figure S1. Correlation coefficient of the soil organic matter, soil water infiltration, soil compaction and soil humidity.

ANNEXE D

Statistical output of the ANOVA and Kruskal-Wallis tests for the soil properties and contaminants in relation to vegetation type

Table S3. Means (± standard error) of soil properties across the different vegetation types in Montreal, Quebec, Canada. Differences between vegetation types were determined with ANOVA or Kruskal-Wallis tests and *post hoc* contrasts with Tukey HSD or Dunn are shown by lowercase letters.

Soil properties	**n**	**Mean (± standard error) rank**				**p**
		Lawns	**Trees**	**Bushes**	**Woodlands**	
SOM (%)	117	21.43 ± 1.47 b	21.72 ± 1.48 b	27.12 ± 2.17 b	37.59 ± 1.69 a	<0.001
Infiltration (cm h^{-1})	114	5.59 ± 0.94 a	5.22 ± 0.77 a	2.40 ± 0.47 b	2.00 ± 0.25 b	<0.001
Humidity (%)	359	19.07 ± 1.25 a	12.39 ± 0.59 c	13.98 ± 0.64 bc	15.46 ± 0.61 b	<0.001
Temperature (°C)	31	23.11 ± 0.46 a	22.01 ± 0.16 ab	21.57 ± 0.39 b	19.74 ± 0.15 c	<0.001
Compaction (kPa)	55	1095 ± 75 a	972 ± 59 a	665 ± 80 b	594 ± 35 b	<0.001
Li	60	0.0057 ± 0.0024	0.0021 ± 0.0007	0.0054 ± 0.0015	0.0026 ± 0.0015	0.283
Na	60	25.20 ± 6.47	38.63 ± 13.84	133 ± 82	6.97 ± 0.72	0.156
Mg	60	120 ± 9	145 ± 23	179 ± 27	167 ± 8	0.135
P	60	0.30 ± 0.05	0.61 ± 0.10	1.85 ± 0.68	1.11 ± 0.67	0.128
K	60	61.32 ± 8.60 b	111 ± 19 ab	171 ± 42 a	63.12 ± 7.43 b	0.005
Zn	60	0	0.072 ± 0.053	0.17 ± 0.13	0.38 ± 0.17	0.063
Pb	60	0.02 ± 0.01	0.01 ± 0.01	0.0055 ± 0.0040	0.030 ± 0.019	0.540
Cu	60	0.13 ± 0.04	0.064 ± 0.010	0.087 ± 0.03	0.031 ± 0.005	0.045

		a	ab	ab	b	
Ba	60	1.82 ± 0.17	2.28 ± 0.41	1.74 ± 0.28	2.09 ± 0.28	0.550

ANNEXE E

List of species identified with (Ellison *et al.*, 2012) who have had nomenclature changed following the book publication

Table S4. List of updated ant species names.

Old species name	Updated species name
Lasius alienus	*Lasius americanus*
Protomognathus americanus	*Temnothorax americanus*
Tetramorium caespitum	*Tetramorium immigrans*

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