Recréer la complexité : diversité végétale et limites écologiques de la restauration des mares de tourbières.

Thèse

Laura Catalina Riano Pena

Doctorat en biologie végétale
Philosophiæ doctor (Ph. D.)

Québec, Canada

Recréer la complexité : diversité végétale et limites écologiques de la restauration des mares de tourbières.

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Sous la direction de :

Line Rochefort, directrice de recherche

Monique Poulin, codirectrice de recherche

Résumé

La restauration des écosystèmes dégradés vise notamment le recouvrement de la biodiversité. Ce projet s'inscrit dans le contexte de la restauration de tourbières dégradées. Les mares, en tant que microformes des tourbières, sont considérées comme des points chauds de biodiversité, car elles abritent des assemblages végétaux et fauniques distincts de ceux associés aux autres microformes des tourbières naturelles. Les microformes de mares sont toutefois fortement affectées par l'extraction de la tourbe, qui entraîne le drainage des sites et la disparition des structures de surface. Depuis plusieurs décennies, plusieurs approches de restauration des tourbières à sphaignes ont été développées pour favoriser le rétablissement du couvert végétal, parmi lesquelles figure notamment la méthode du transfert de la couche muscinale. Toutefois, malgré ces interventions, les mares restaurées présentent encore fréquemment des caractéristiques morphologiques simplifiées et une végétation moins diversifiée que celle observée dans les systèmes naturels. Parallèlement, des mares spontanées peuvent se former naturellement, mais le retour spontané de la composition des communautés végétales demeure encore peu documenté. Cette thèse vise à mieux décrire la diversité végétale associée aux mares dans les tourbières de référence (naturelles) et restaurées, ainsi que les facteurs environnementaux qui influencent leur assemblage, afin d'évaluer dans quelle mesure la restauration permet de recréer les habitats de mares et de favoriser le retour des communautés végétales spécialisées. Les analyses ont été réalisées dans des tourbières ombrotrophes et minérotrophes situées dans l'est et l'ouest du Canada. La végétation a été inventoriée le long de gradients perpendiculaires aux mares, depuis l'eau jusqu'à 10 m dans le milieu adjacent. Les conditions environnementales des mares ont été caractérisées à l'aide de variables spatiales, morphologiques et chimiques. Les résultats montrent que la morphologie des mares influence fortement la composition et la diversité végétale dans les tourbières ombrotrophes, en agissant comme un filtre écologique. Les mares peu profondes favorisent des espèces vasculaires généralistes (p. ex. *Typha latifolia*) au détriment des mousses spécialisées (p. ex. *Sphagnum* spp.), entraînant une augmentation de la diversité bêta le long du gradient de profondeur des mares (entre mares peu profondes et profondes), ainsi qu'une diminution de la spécificité des assemblages. Dans les tourbières minérotrophes, les types de mares expliquent davantage la variabilité des communautés que les gradients régionaux, suggérant un rôle central des conditions locales et du type de mare dans la structuration de la végétation. L'étude du gradient hydrologique du bord de la mare vers l'étendue de la tourbière ombrotrophe montre que la composition végétale varie systématiquement avec la distance à la mare, mais que ce patron dépend du type de mare. Les mares créées présentent une augmentation de la richesse avec le temps, sans convergence complète vers les communautés de référence, tandis que les mares spontanées, bien que moins riches, présentent une composition plus proche des conditions naturelles. Dans l'ensemble, ces résultats indiquent que le design de création des mares ne permet pas encore de restaurer pleinement les communautés végétales caractéristiques des tourbières naturelles. Ma thèse souligne

l'importance de considérer à la fois les conditions environnementales locales associées aux mares, le type de mare, ainsi que les processus liés à la dynamique des communautés végétales dans les stratégies de restauration, notamment par le biais d'interventions ciblées favorisant les espèces spécialistes.

Abstract

Restoration of degraded ecosystems aims, among other goals, to recover biodiversity. This project is situated within the context of peatland restoration. Pools, as microforms of peatlands, are considered biodiversity hotspots because they host plant and faunal assemblages that differ from those associated with other microforms in natural peatlands. However, pool microforms are strongly affected by peat extraction, which leads to site drainage and the loss of surface structures. Over the past several decades, various approaches to restoring Sphagnum peatlands have been developed to promote vegetation recovery, including the moss layer transfer technique. Nevertheless, restored pools still frequently exhibit simplified morphological characteristics and less diverse vegetation than that observed in natural systems. In parallel, spontaneous pools can form naturally, but the spontaneous recovery of plant community composition remains poorly documented. This thesis aims to better describe the plant diversity associated with pools in reference (natural) and restored peatlands, as well as the environmental factors influencing their assemblages, in order to assess the extent to which restoration can recreate pool habitats and promote the return of specialized plant communities. Analyses were conducted in ombrotrophic and minerotrophic peatlands located in eastern and western Canada. Vegetation was surveyed along transects perpendicular to pools, from the water edge to 10 m into the surrounding peatland. Environmental conditions of pools were characterized using spatial, morphological, and chemical variables. The results show that pool morphology strongly influences plant composition and diversity in ombrotrophic peatlands by acting as an ecological filter. Shallow pools favour generalist vascular species (e.g. *Typha latifolia*) at the expense of specialized bryophytes (e.g. *Sphagnum* spp.), leading to increased beta diversity along the pool depth gradient (between shallow and deep pools), as well as reduced community specificity. In minerotrophic peatlands, pool types explain more of the variation in communities than regional gradients, suggesting a central role of local conditions and pool type in structuring vegetation. The study of the hydrological gradient from pool margins into the surrounding ombrotrophic peatland shows that vegetation composition varies systematically with distance from pools, but that this pattern depends on pool type. Constructed pools show an increase in species richness over time without full convergence toward reference communities, whereas spontaneous pools, although less species-rich, exhibit a composition more similar to natural conditions. Overall, these results indicate that current pool creation designs do not yet fully restore the plant community's characteristic of natural peatlands. This thesis highlights the importance of considering local environmental conditions associated with pools, pool type, and community assembly processes in restoration strategies, particularly through targeted interventions promoting specialist species.

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< Mi madre me mostró que el acto más valiente era creer en mí misma. Mi familia, mis compañeras y compañeros de camino, me mostraron la fuerza irresistible de la convicción y Colombia me mostró que la utopía sirve para caminar. >

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Avant-propos

Cette thèse se compose de cinq parties, dont une introduction générale, trois chapitres et une conclusion. Les trois chapitres centraux sont rédigés sous la forme d'articles scientifiques dont je suis la première auteure. Pour chacun de ces articles, j'ai défini les objectifs et hypothèses de recherche, conçu la méthodologie, collecté les données, réalisé les analyses statistiques et rédigé les manuscrits. Line Rochefort et Monique Poulin ont supervisé l'ensemble de cette thèse et ont contribué activement à la révision du manuscrit. De plus, Mélina Guêné-Nachen et Philippe Janssen sont coauteurs des chapitres 1, 2 et 3 et ont également collaboré à l'analyse des données et à la conception des articles. Le chapitre 1 a été publié dans *Botany* en février 2026. Le chapitre 2 sera soumis à la revue *Restoration Ecology* avec le même format que celui de la thèse. Le chapitre 3 sera soumis dans un format légèrement différent de celui présenté dans cette thèse. Aussi, avec l'accord de ma directrice, des outils d'intelligence artificielle générative (IA) ont été utilisés à diverses étapes du processus de recherche et les contenus qu'ils ont générés ont été systématiquement contre-vérifiés. Les outils d'IA générative ont servi à soutenir la correction de la rédaction en anglais. Pour la revue de littérature, ces outils ont facilité la synthèse d'articles préalablement analysés et l'organisation thématique des sources. Finalement, ils ont été utilisés pour l'amélioration au niveau du codage statistique. À tout moment, j'ai assuré la protection de la confidentialité des données en utilisant un outil d'IA sécurisé.

Chapitre 1 (publié le 3 février 2026) : Riaño Peña, L. C. R., Guêné-Nanchen, M., Janssen, P., Poulin, M., & Rochefort, L. (2026). Environmental influences on plant diversity in restored and natural peatland pools. *Botany*, *104*, 1-26.

Chapitre 2 : Riaño Peña L.C., Guêné-Nanchen M., Janssen P., Poulin M. et Rochefort L., Where the Water Settles: Exploring the Ecological Drivers of Plant Communities in Restored Minerotrophic Peatland Pools.

Chapitre 3 : Riaño Peña L.C., Guêné-Nanchen M., Janssen P., Poulin M., et Rochefort L., Divergent plant recovery along a hydrological gradient in restored *Sphagnum*-dominated peatland pools.

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- Symposium scientifique du Groupe de recherche en écologie des tourbières (GRET) et SER-EC, Université Laval, Québec, avril 2022.
- Workshop sur le suivi de la restauration écologique des tourbières, Université du Manitoba, Winnipeg, juin 2022.
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- Symposium Centre de recherche et d'innovation sur les végétaux, Université Laval, Québec, octobre 2024.
- Symposium scientifique du Groupe d'études en écologie des tourbières (GRET), Université Laval, Québec, février 2026.

Introduction

Problématique

Le Canada possède la deuxième plus grande superficie de tourbières au monde (UNEP, 2022). Au Québec, elles couvrent environ 9 à 12 % du territoire, soit près de 118 000 km² (Payette et Rochefort, 2001), et représentent les milieux humides les plus abondants de la province, constituant environ 85 % de l'ensemble des milieux humides au Québec (Pellerin et Poulin, 2013). On distingue principalement deux types de tourbières : les ombrotrophes, ou bogs, dominées par les sphaignes, et les minérotrophes, ou fens. Les paysages des tourbières présentent également une mosaïque de microformes, parmi lesquelles les mares occupent une place importante. Ces plans d'eau sont souvent considérés comme des points chauds pour la biodiversité, car ils abritent des assemblages d'espèces végétales et animales distincts de ceux retrouvés dans le reste de la tourbière (Standen et al., 1998).

Au Québec, les tourbières ont subi diverses perturbations au cours des dernières décennies, principalement générées par des activités reliées à la production agricole, aux activités sylvicoles, à l'hydroélectricité et, dans une moindre mesure, à l'extraction de la tourbe (Poulin et al., 2004; Pellerin et Poulin, 2013). L'extraction de la tourbe à des fins horticoles nécessite le drainage de la tourbière et le décapage de l'acrotelme (Price et al., 2003; Rochefort et al., 2016), ce qui entraîne la disparition de microformes comme les mares et, par conséquent, la perte de la biodiversité associée à ces microformes à l'échelle locale (Donahue et al., 2022; Koivunen et al., 2023). Afin de compenser ces pertes, des travaux de restauration écologique des tourbières sont réalisés depuis plus de trente ans et incluent parfois la création des mares afin de rétablir certaines composantes de la biodiversité (Quinty et Rochefort, 2003).

La restauration écologique vise le rétablissement des communautés végétales et des fonctions écologiques des tourbières (González et al., 2014; Nugent et al., 2018). Toutefois, les techniques de restauration ont été principalement développées pour les tourbières ombrotrophes et les techniques de restauration des tourbières minérotrophes sont en cours de développement (Rochefort et al., 2016; Khan et al., 2025). La création des mares fait partie des approches pour favoriser la biodiversité dans les tourbières restaurées. Cependant, les paramètres de conception ont surtout porté sur l'imitation de la morphologie des mares naturelles (ou de référence), sans toujours inclure des stratégies adaptées pour la réintroduction des espèces végétales typiques des mares (Quinty et Rochefort, 2003). Il demeure donc nécessaire d'approfondir les connaissances sur l'écologie et la biologie des espèces aquatiques et semi-aquatiques associées aux mares, notamment en ce qui concerne les processus de colonisation spontanée, afin de mieux comprendre les dynamiques de retour de la végétation et d'orienter les stratégies de gestion et de restauration.

Dans ce contexte, ce projet de doctorat porte sur la recolonisation spontanée des espèces végétales dans les mares de tourbières restaurées. Plus précisément, il vise à comprendre la composition et la richesse des communautés végétales colonisant ces microformes, ainsi que les variables environnementales qui influencent leur établissement. Cette recherche se décline en trois objectifs principaux : (1) identifier les variables environnementales influençant la richesse et le recouvrement des espèces végétales dans différents types de mares situées dans des tourbières ombrotrophes restaurées comparées à celles des mares de référence; (2) évaluer l'influence des variables environnementales locales et des facteurs régionaux sur l'établissement de la végétation dans les mares de référence et les tourbières minérotrophes restaurées comparées à celles des mares de référence; et (3) analyser l'effet du gradient perpendiculaire et du temps sur le rétablissement de la végétation dans les mares des tourbières restaurées ombrotrophes comparées à celles des mares de référence. Ce projet contribuera ainsi à améliorer les connaissances fondamentales sur la colonisation des mares en tourbières restaurées et à soutenir le développement de pratiques de restauration plus efficaces pour ces microformes, tout en permettant de caractériser, à partir d'inventaires floristiques, les différences entre mares et platières et d'évaluer si les mares constituent des points chauds de diversité floristique.

Développement et présence des mares en tourbières ombrotrophes et minérotrophes

Les mares constituent des éléments structurants du paysage des tourbières. Leur développement résulte d'interactions complexes entre hydrologie, microtopographie, dynamique de la tourbe et facteurs climatiques. Même si les mécanismes varient selon le contexte biogéographique, un point fait consensus : les mares s'initient généralement dans des dépressions préexistantes où l'eau peut s'accumuler, puis évoluent lentement par des processus autogènes et allogènes combinés (Foster et Fritz, 1987; Foster et al., 1988).

Dans les tourbières boréales et tempérées sans pergélisol, les mares apparaissent le plus souvent dans des creux issus de la différenciation microtopographique entre crêtes et dépressions (Foster et Wright, 1990). Cette différenciation découle de taux d'accumulation de tourbe contrastés, liés à la composition végétale et aux conditions hydriques (Foster et al., 1988). Les espèces présentes sur les crêtes (e.g., *Sphagnum fuscum*) sont généralement plus résistantes à la décomposition, favorisant une accumulation verticale plus rapide que dans les dépressions (Bengtsson et al., 2016; Turetsky et al., 2008).

Trois grands modèles de formation ont été proposés (Foster et Wright, 1990). Le premier suggère une formation précoce, dès les premières phases d'accumulation de la tourbe. Toutefois, la présence fréquente de tourbe sous les mares actuelles indique plutôt une formation postérieure au développement initial de la tourbière (Loisel et al., 2017). Le modèle autogène propose que les mares apparaissent au centre d'une

tourbière en croissance, puis s'étendent latéralement avec l'expansion du dôme tourbeux (Foster et Wright, 1990 ; Belyea et Lancaster, 2002). Leur dynamique serait alors principalement contrôlée par la morphologie et l'hydrologie internes. Le modèle allogène suggère, au contraire, une formation déclenchée par des facteurs externes, notamment d'ordre climatique (Foster et Wright, 1990). Par exemple, une hausse significative des précipitations peut entraîner une remontée de la nappe phréatique, noyer les dépressions existantes et favoriser leur expansion par décomposition (Arlen-Pouliot et Payette, 2015).

Une fois initiées, les mares évoluent par expansion latérale et s'approfondissent. Plusieurs mécanismes ont été proposés pour expliquer leur croissance horizontale : coalescence de mares voisines (Foster et al., 1988), érosion des marges sous l'action du vent et des vagues (Pearsall, 1956), écoulement préférentiel à travers des zones à forte conductivité hydraulique (Ingram, 1982). Les patrons spatiaux observés peuvent refléter ces mécanismes. Dans les tourbières qui présentent une pente marquée, par exemple, les tourbières de couverture (blanket bogs), les mares ont tendance à s'allonger perpendiculairement au gradient topographique, ce qui limite leur expansion latérale (Foster et Glaser, 1986; Belyea, 2007; Rydin et Jeglum, 2013). La coalescence progressive des mares adjacentes peut conduire à la formation de grandes surfaces en eau ou formant parfois des flarks allongés perpendiculaires à la pente. Des observations bathymétriques ont mis en évidence des crêtes résiduelles sous certaines mares, correspondantes à d'anciennes lanières de tourbe, témoins de cette fusion graduelle (Foster et Fritz, 1987).

D'un autre côté, l'approfondissement des mares est lié aux conditions physico-chimiques dans la colonne d'eau. Comparativement à la tourbe saturée environnante, l'eau libre présente une plus grande pénétration lumineuse, des températures plus élevées en surface et des concentrations en oxygène supérieures (Foster et Glaser, 1986; Hamilton et al., 1994; Karofeld et Tõnisson, 2014). Ces conditions stimulent l'activité microbienne à l'interface eau-tourbe, accélérant la décomposition de la matière organique et ralentissant l'accumulation relative de tourbe dans les mares (Belyea et Clymo, 1998; Belyea et Lancaster, 2002). En général, la profondeur des mares dépasse rarement deux mètres, car au-delà les concentrations en oxygène deviennent limitantes pour la décomposition (Hamilton et al., 1994; McEnroe et al., 2009). Des rétroactions biologiques peuvent aussi intervenir. La présence de cyanobactéries benthiques pourrait augmenter localement la disponibilité en oxygène et en azote, stimulant ainsi l'activité microbienne et contribuant au dynamisme morphologique des mares (Hamard et al., 2021; Hamilton et al., 1994).

Le développement des mares est un processus lent, s'étendant sur des siècles ou des millénaires (Belyea et Lancaster, 2002). Toutefois, à l'échelle décennale, des changements dans leur nombre et leur organisation spatiale ont été observés à partir d'analyses diachroniques et d'images aériennes (Arlen-Pouliot et Payette, 2015). Les mares peuvent également régresser. Le drainage par des canaux est documenté, particulièrement dans les tourbières à forte pente (Foster et al., 1988; Holden et al., 2018). Une baisse prolongée de la nappe

phréatique liée à l'augmentation de l'évapotranspiration sous un climat plus chaud peut aussi entraîner leur assèchement (Arsenault et al., 2019). Enfin, la formation des tapis flottants issus du dégazage de méthane peut favoriser leur comblement progressif (Strack et al., 2005).

Finalement, les mécanismes fondamentaux d'initiation, d'accumulation d'eau dans des dépressions microtopographiques et de différenciation des taux d'accumulation de tourbe sont communs aux tourbières ombrotrophes et minérotrophes (Foster et al., 1988). Cependant, leur importance relative dépend fortement du type de tourbière. Dans les bogs, alimentés uniquement par les précipitations, la dynamique interne du dôme et les rétroactions autogènes jouent un rôle central (Foster et Wright, 1990 ; Glaser et Janssens, 1986). L'organisation spatiale des mares y est fortement structurée par la morphologie et la pente de la tourbière. Dans les fens, les apports d'eau souterraine rendent le système plus sensible aux variations du régime hydrologique régional. Les processus allogéniques, notamment les changements climatiques à long terme, peuvent y exercer un contrôle plus direct sur la formation et l'expansion des mares (Arlen-Pouliot et Payette, 2015). La chimie plus riche en eau des fens peut également modifier les taux de production et de décomposition, influençant la vitesse d'évolution des mares (Geurts et al., 2010). C'est pour cette raison qu'une analyse détaillée des caractéristiques des mares, incluant la chimie de l'eau, la morphologie, la biodiversité et l'hydrologie, constitue une étape essentielle pour comprendre leur dynamique interne et leur contribution au fonctionnement global des tourbières.

Les mares et leur contribution aux tourbières

Les tourbières représentent l'un des milieux humides les plus importants de l'hémisphère nord et jouent un rôle majeur dans le stockage du carbone (Harris et al., 2022; Nichols et Peteet, 2019), la régulation hydrologique (Whittington et Price, 2006; Waddington et al., 2015; Goodbrand et al., 2019) et le maintien de la biodiversité (Aapala et al., 2014; Tanneberger et al., 2021). Ces milieux se caractérisent par l'accumulation de matière organique partiellement décomposée sous forme de tourbe, résultant des conditions saturées en eau et d'une faible décomposition biologique (Payette et Rochefort, 2001). À l'échelle mondiale, les tourbières couvrent une proportion relativement faible, environ 3 à 4 %, de la surface terrestre (Minasny et al., 2024; UNEP, 2022; Xu et al., 2018), mais elles contiennent une part disproportionnée du carbone des sols, ce qui en fait l'un des principaux réservoirs terrestres de carbone et un régulateur majeur du climat global via le stockage à long terme du carbone et l'influence sur les flux de CO_2 et CH_4 (Gorham, 1991; Yu, 2012). On distingue principalement deux types de tourbières selon leur alimentation hydrologique : les bogs, alimentés uniquement par les précipitations, pauvres en éléments minéraux et dominés par les sphaignes, et les fens, hydrologiquement connectés aux eaux de surface ou souterraines et caractérisés par un gradient de richesse en nutriments, allant de conditions pauvres à très riches, avec une végétation incluant mousses brunes et

graminoïdes comme les *Carex* (Vitt, 2006; Rydin et Jeglum, 2013). Ces différences hydrologiques et chimiques, notamment en termes de pH, de conductivité et de concentration en nutriments (azote, phosphore), influencent la composition végétale, la dynamique de la tourbe et la formation de microformes, dont les mares, qui contribuent à la biodiversité des tourbières.

Pour certaines tourbières, les mares constituent des microformes structurantes importantes du paysage. Ces microformes, d'origine secondaire à la formation de la tourbière, se développent généralement dans des dépressions microtopographiques où l'eau s'accumule, sous l'influence conjointe de facteurs hydrologiques, biologiques et climatiques (Foster et Fritz, 1987; Foster et al., 1988). Dans les tourbières boréales, leur formation est souvent liée à la différenciation entre les buttes et les dépressions, due à des taux contrastés d'accumulation de tourbe, associés à la végétation et aux conditions hydriques (Belyea et Clymo, 2001). Leur origine peut être expliquée par des processus autogènes, liés à la dynamique interne de la tourbière, ou allogènes, déclenchés par des facteurs externes comme les variations climatiques et hydrologiques (Foster et Wright, 1990; Arlen-Pouliot et Payette, 2015). Une fois formées, les mares évoluent lentement par expansion latérale, notamment par coalescence ou érosion des marges, et par approfondissement dû à une décomposition accrue de la tourbe à l'interface eau-tourbe, favorisée par des conditions physico-chimiques plus favorables pour l'activité microbienne (Belyea et Clymo, 1998; Hamilton et al., 1994; Karofeld, 1998, Belyea et Lancaster, 2002).

La présence des mares contribue à créer une mosaïque d'habitats aquatiques et semi-aquatiques qui augmente l'hétérogénéité écologique des tourbières (Lindsay, 2010; Beadle et al., 2015; Graham et al., 2020; Couwenberg et al., 2022). Cette hétérogénéité favorise le développement d'une diversité d'organismes adaptés à des conditions environnementales variées (Figure 1). Les mares peuvent ainsi servir d'habitats pour différentes espèces de plantes (Fontaine et al., 2007; Riaño Peña et al., 2026), d'invertébrés (Batzer et al., 2016; Drapeau Picard et al., 2021), d'amphibiens (Mazerolle, 2005; Mazerolle et al., 2006; Stückler et al., 2024) et de microorganismes (Gilbert et al., 1999; Li et al., 2022). Les mares influencent également la dynamique hydrologique des tourbières en contribuant à la circulation et au stockage de l'eau à l'échelle locale, et peuvent jouer un rôle dans les échanges de gaz à effet de serre, notamment la production de méthane, selon les conditions de décomposition anaérobie de la matière organique (Beadle et al., 2015; Holden et al., 2018; Taillardat et al., 2024). Cependant, les mares des tourbières sont particulièrement sensibles aux perturbations environnementales. Les activités anthropiques telles que le drainage modifient profondément les conditions hydrologiques qui régissent leur formation et leur maintien (Beadle et al., 2015; Holden et al., 2017). Ces modifications peuvent entraîner des variations sur la morphologie et le fonctionnement écologique des mares.

La dynamique des mares est influencée par des perturbations naturelles, comme les variations saisonnières du niveau d'eau, et par des perturbations anthropiques, telles que le drainage ou le pâturage. Dans cette thèse, l'accent est mis sur la caractérisation des mares et de leur végétation, afin de mieux comprendre leur rôle en termes de biodiversité et d'orienter les stratégies de gestion et de restauration des tourbières.

Dégradation et restauration des tourbières

Les tourbières sont des écosystèmes particulièrement sensibles aux perturbations anthropiques, en raison de leur hydrologie spécifique et de leur lente accumulation de matière organique. Au Canada, ces milieux ont été affectés par diverses activités humaines, notamment le drainage à des fins agricoles, les activités forestières et l'inondation liée au développement hydroélectrique (Chapman et al., 2003; Joosten et Clarke, 2002; Pellerin et Poulin, 2013). Bien que l'extraction de la tourbe occupe des superficies relativement limitées à l'échelle du territoire, elle peut néanmoins entraîner des impacts écologiques importants (Poulin et al., 2004; Rochefort et al., 2022). Dans les tourbières ombrotrophes (bogs), l'extraction de la tourbe peut réduire significativement la superficie des tourbières à l'échelle régionale et mener à la disparition de certaines composantes caractéristiques du paysage, telles que les mares des tourbières (Poulin et al., 2004).

L'extraction de la tourbe implique généralement plusieurs étapes qui modifient la structure et le fonctionnement des tourbières. Ces opérations incluent la construction des canaux de drainage afin d'abaisser le niveau de la nappe phréatique, ainsi que l'enlèvement de la végétation de surface et des couches supérieures de tourbe (Price et al., 2003; Rochefort et al., 2016). Ces interventions perturbent les processus hydrologiques et écologiques qui soutiennent le fonctionnement des tourbières, empêchent la recolonisation des espèces typiques des tourbières et favorisent l'établissement des conditions environnementales très différentes de celles observées dans les systèmes naturels (p. ex. Price et al., 2003; Frolking et al., 2011; Renou-Wilson et al., 2019).

Après l'extraction de la tourbe, la recolonisation des plantes est lente et incertaine. Les espèces végétales peuvent prendre plusieurs décennies pour recoloniser les tourbières perturbées, et certaines d'entre elles peuvent ne jamais revenir (Poulin et al., 2005; Allan et al., 2024). De plus, les modifications des conditions abiotiques peuvent favoriser la colonisation des espèces atypiques, différentes de celles observées dans les tourbières naturelles (aussi appelées écosystèmes de référence; Graf et al., 2008; Pasquet et al., 2015). En conséquence, les tourbières post-extraction présentent souvent des différences marquées par rapport à leur état initial, tant en termes de composition en espèces que de fonctionnement écologique, ce qui limite leur capacité à soutenir la biodiversité et les services écosystémiques associés aux tourbières.

Face à ces enjeux, la restauration écologique est devenue une approche essentielle pour favoriser le rétablissement des tourbières. L'objectif de la restauration est de rétablir des écosystèmes fonctionnels

capables de soutenir la biodiversité et de fournir des services écosystémiques essentiels (González et al., 2014; Nugent et al., 2018). Depuis les années 1990, d'importants efforts ont été consacrés au développement de méthodes de restauration adaptées aux tourbières, en particulier pour les bogs. Parmi ces approches, la méthode de transfert de la couche muscinale ou MTCM (*Moss Layer Transfer Technique*, *MLTT*) est aujourd'hui l'une des méthodes les plus utilisées (Rochefort et al., 2003). Cette technique consiste à réintroduire du matériel végétal provenant de sites donneurs, principalement des fragments de sphaignes et d'autres bryophytes associées, à la surface de la tourbe résiduelle (Graf et Rochefort, 2016). Cette intervention est généralement accompagnée d'autres actions, telles que la préparation de la surface de la tourbe, des modifications topographiques visant à améliorer la distribution de l'eau et le blocage des canaux de drainage afin de rétablir les conditions hydrologiques (Quinty et Rochefort, 2003; Landry et Rochefort, 2011). Dans des conditions favorables, cette méthode permet le rétablissement de la végétation typique des tourbières en cinq à dix ans environ, accélérant considérablement les processus naturels de recolonisation (González et al., 2014).

Malgré les progrès réalisés dans le domaine de la restauration des tourbières, le rétablissement complet de la structure et du fonctionnement de ces écosystèmes demeure un défi. Certains éléments structurants du paysage, tels que les mares, peuvent être particulièrement difficiles à rétablir, et leur structure après la restauration reste encore relativement peu comprise.

Homogénéisation biotique : la restauration écologique peut-elle ne pas prendre la bonne voie?

Les perturbations des écosystèmes causées par les activités anthropiques favorisent souvent une tendance croissante vers l'homogénéisation biotique, un processus par lequel des communautés biologiques auparavant distinctes deviennent de plus en plus similaires dans leur composition en espèces (McKinney et al., 1999; Olden et al., 2004; Solar et al., 2015; Socolar et al., 2016). Cette dynamique résulte souvent de la disparition d'espèces spécialisées et de la colonisation d'espèces généralistes capables de tolérer une plus grande variabilité des conditions environnementales (Filgueiras et al., 2021; McKinney et Lockwood, 1999). La restauration écologique est fréquemment présentée comme une stratégie pour contrer cette tendance en rétablissant des écosystèmes plus proches de leur état naturel (SER, 2004; Gann et al., 2019; Moreno-Mateos et al., 2020). Toutefois, dans les projets de restauration impliquant une revégétalisation active, les interventions sont souvent conçues et évaluées à partir d'indicateurs locaux, tels que la couverture végétale ou la richesse spécifique à l'échelle du site (diversité alpha) (Wortley et al., 2013; Evju et al., 2020). Une telle approche peut mener à l'établissement de communautés relativement similaires entre les sites restaurés, limitant ainsi le retour de la diversité biologique à l'échelle régionale (diversité bêta) (p. ex. Sapkota et al.,

2021; Lane et al., 2022). Dans les tourbières, cette question est particulièrement pertinente, car les perturbations liées à l'extraction de la tourbe modifient les conditions et la structure des microformes, telles que les mares. La restauration des tourbières vise le rétablissement de la végétation typique des tourbières en général, mais elle ne se concentre pas sur les microformes spécifiques, et la végétation typique des mares ne revient pas spontanément, même après six ans post-restauration (Fontaine et al., 2007; Riaño Peña et al., 2026). La recolonisation végétale des mares après la restauration demeure un enjeu important pour soutenir la biodiversité à l'échelle du paysage.

Comprendre la structure des communautés pour orienter la restauration des mares de tourbière

La restauration écologique vise généralement à rétablir des écosystèmes capables de soutenir des communautés biologiques diversifiées (Benayas et al., 2009; Miller et al., 2017). Toutefois, le succès des projets de restauration ne se limite pas au rétablissement des conditions physiques du milieu, mais dépend également de la capacité des espèces à recoloniser les habitats restaurés (Cornell et Lawton, 1992; Sundermann et al., 2011). La structure des communautés biologiques constitue donc un élément clé pour évaluer l'état écologique des écosystèmes restaurés, car elle reflète les processus écologiques sous-jacents tels que le filtrage environnemental, les limitations de dispersion, la succession et les interactions biotiques qui régissent le rétablissement et la distribution des espèces (Godoy et al., 2024).

Dans les écosystèmes aquatiques tels que les mares, la structure des communautés peut être décrite à l'aide de plusieurs indicateurs écologiques, notamment la richesse spécifique, l'abondance relative des espèces et la composition floristique (Magurran, 2005). Ces indicateurs permettent de caractériser l'organisation des communautés biologiques. L'étude de la biodiversité à différentes échelles spatiales, par exemple au moyen des concepts de diversité alpha, bêta et gamma, offre également un cadre conceptuel utile pour comprendre la structuration des communautés (Whittaker, 1972; González-Megías et al., 2007).

Dans les tourbières, l'hétérogénéité des microformes, incluant les mares, les bosquets d'arbres, les buttes et les dépressions, contribue à créer une mosaïque d'habitats qui peut soutenir une diversité biologique importante (Chroňáková et al., 2019; Graham et al., 2020). Les mares, en particulier, constituent des habitats aquatiques susceptibles d'accueillir des assemblages d'espèces différents de ceux observés dans les zones plus sèches des tourbières (Mazerolle et al., 2006; Fontaine et al., 2007). Les conditions environnementales propres à ces microformes, telles que la profondeur et la chimie de l'eau, la stabilité de la nappe phréatique ou encore les caractéristiques du substrat, influencent fortement la composition des communautés végétales et leur distribution (Holden et al., 2016; Arsenault et al., 2018; Jolin et al., 2024). Cependant, ces connaissances restent limitées : la plupart des études portent sur un nombre restreint de sites et examinent

souvent ces facteurs de manière isolée. La présente thèse vise à proposer une approche plus intégrée et étendue, afin de mieux caractériser l'influence combinée de ces variables sur la végétation des mares en tourbières restaurées ombrotrophes et minérotrophes.

Comprendre comment ces facteurs environnementaux et biologiques structurent les communautés est essentiel pour orienter les stratégies de restauration écologique. En effet, les réponses des espèces aux conditions abiotiques, leurs capacités de dispersion et leurs interactions écologiques se reflètent dans les patrons de composition des communautés observés dans les écosystèmes restaurés. Une meilleure connaissance de ces relations permet ainsi de mieux interpréter les mécanismes potentiels à l'origine de ces patrons et d'améliorer la planification des interventions de restauration.

Création des mares en tourbières restaurées : un ajout pour la biodiversité

La création des mares constitue une pratique courante lors de la restauration des tourbières afin d'augmenter l'hétérogénéité des habitats et de favoriser la biodiversité (Beadle et al., 2015). Le guide de restauration de tourbières (Quinty et Rochefort, 2003) recommande d'aménager ces plans d'eau après l'extraction de la tourbe, afin de fournir des habitats pour la faune et de diversifier la microtopographie présente dans les tourbières restaurées. En général, il est suggéré de créer des mares d'une superficie d'environ 75 à 150 m², ce qui permet d'offrir un habitat adéquat pour différentes espèces. Une profondeur d'environ 1 à 2 mètres est également préconisée afin de maintenir la présence d'eau pendant toute la saison de croissance. La morphologie idéale comprend des pentes asymétriques, avec un côté plus abrupt et l'autre plus graduel, afin de recréer la morphologie des mares naturelles et de permettre à la faune de pouvoir aisément entrer et sortir du plan d'eau.

Dans la pratique, les mares créées présentent toutefois souvent des caractéristiques différentes de celles recommandées. Leur excavation à l'aide de la machinerie lourde produit fréquemment des formes plus anguleuses et des berges majoritairement plus abruptes. De plus, la présence d'eau dans ces mares dépend en grande partie du succès des interventions de remise en eau du site plutôt qu'uniquement de leur taille ou de leur profondeur (Haapalehto et al., 2011; Holden et al., 2018). Les conditions hydrologiques des tourbières restaurées peuvent également différer de celles de référence. Par exemple, le niveau de la nappe phréatique peut y être plus fluctuant, ce qui entraîne des variations de la superficie des mares au cours de la saison et peut parfois provoquer leur assèchement temporaire (Whittington et Price, 2006; Holden et al., 2018). Dans les tourbières ombrotrophes, la colonisation végétale peut varier considérablement selon les conditions présentes après la restauration (Beadle et al., 2015; Arsenault et al. 2019). Les mousses du genre *Sphagnum* contribuent à retenir l'eau et à stabiliser le niveau de la nappe, même en période de sécheresse (Brown et

al., 2010). À l'inverse, la décomposition de certaines matières végétales, comme les feuilles de mélèze riches en azote, peut enrichir le milieu en nutriments et accélérer certains processus biogéochimiques associés aux mares, comme la minéralisation de la matière organique et la production de nutriments disponibles pour les plantes (Carlyle et Malcolm 1986; Arsenault et al. 2019).

Lors des travaux de restauration, les anciens canaux de drainage sont généralement bloqués, mais ils ne sont pas toujours complètement comblés de tourbe, ce qui permet l'accumulation de l'eau au fil du temps. Cette accumulation entraîne la formation de surfaces d'eau libre qui peuvent favoriser la colonisation d'une végétation hydrophyte (Minkkinen et Laine, 2006). Dans ce contexte, l'obstruction des canaux de drainage peut mener à la formation de plans d'eau, appelés aussi « mares ». L'eau peut également s'accumuler dans des dépressions créées par le passage de la machinerie lourde ou dans les zones topographiquement plus basses de la tourbière. Avec le temps, ces dépressions peuvent être progressivement colonisées par la végétation, conduisant à la formation de mares spontanées. La végétation colonisant les canaux de drainage et les mares spontanées demeure peu documentée et sa contribution à la biodiversité des tourbières restaurées reste inexplorée (Figure 1).

Revégétalisation des berges de mares

Dans les tourbières ombrotrophes restaurées, plusieurs études ont examiné l'établissement de la végétation autour des mares créées. Les premières observations ont montré que la recolonisation spontanée de la végétation associée aux mares pouvait demeurer très limitée pendant plusieurs années après la restauration, avec peu ou pas de reprise même six ans après les efforts de restauration (Fontaine et al., 2007). Ces constats ont mené au développement de techniques visant à favoriser l'établissement des espèces typiques des mares des tourbières. Par exemple, la germination des plantes vasculaires semble être favorisée par un niveau d'eau proche de la surface, ainsi que par la présence de substrats de tourbe nu ou de tapis de *Sphagnum* (Landry et al., 2012). D'autres travaux ont également montré que le succès de la restauration peut être amélioré en combinant l'ensemencement d'espèces vasculaires avec l'épandage de fragments de bryophytes et l'introduction d'espèces d'hépatiques comme *Odontoschisma fluitans* (Laberge et al., 2015). Dans les tourbières minérotrophes, certaines interventions incluent aussi la réintroduction des plantes, notamment des carex et des bryophytes. Ces actions ont généralement permis l'établissement d'un couvert végétal caractéristique des tourbières minérotrophes (Bourgeois et al., 2018; Drapeau Picard et al., 2021). Toutefois, au-delà des conditions environnementales et des interventions de restauration, l'établissement des plantes autour des mares dépend également de la capacité des espèces à se disperser dans le paysage et à coloniser les sites. Les mécanismes de dispersion des propagules et certains traits biologiques des espèces peuvent ainsi jouer un rôle important dans la structuration des communautés végétales (Campbell et al., 2003; Merritt et al., 2010; Wang et al., 2019). Par ailleurs, l'établissement des mousses peut également influencer

les dynamiques de régénération en agissant comme filtre biotique, notamment en réduisant la germination de certaines espèces vasculaires comme *Typha latifolia*, un effet observé dans des contextes de bogs et de fens restaurés (Bourgeois et al., 2012).

Les mares peuvent-elles être considérées comme étant de petits écosystèmes jouant des rôles significatifs (*small natural features*)?

Les « *small natural features* » (SNF) ont une influence écologique remarquable. Ce sont des sites dont l'importance écologique est disproportionnée par rapport à leur taille, car ils fournissent des ressources essentielles qui permettent l'établissement de populations clés. Ils favorisent une diversité, une abondance ou une productivité inhabituellement élevée, et reproduisent à petite échelle certaines fonctions des écosystèmes naturels (Hunter, 2005; Hunter et al., 2017). Les caractéristiques physiques des SNF peuvent varier. Selon Goves et Game (2016), ils peuvent être naturels, comme la végétation riveraine, ou associés à des milieux restaurés. Dans ce dernier cas, ils sont généralement similaires aux écosystèmes comparables. Par exemple, les milieux humides temporaires soutiennent la végétation et la faune le long des cours d'eau dans des environnements arides (Acuña et al., 2017; Calhoun et al., 2017; Cheng et al., 2023). Malgré leur petite taille, ces SNF constituent souvent les seules oasis de végétation semi-naturelle ou de services écosystémiques spécifiques dans des paysages dégradés ou en processus de restauration (Hunter, 2017; Lundquist et al., 2017). Les SNF concentrent souvent des ressources limitées mais critiques, comme l'eau. Dans les régions arides et semi-arides, les sources désertiques en sont un exemple (Brendonck et Williams, 2000; Arthington et al., 2005; Davis et al., 2013). Même dans des régions humides, les masses d'eau stagnantes ou courantes peuvent être rares, au moins saisonnièrement, limitant et structurant la distribution du biote aquatique et semi-aquatique (Douglas et al., 2005; González del Tánago et al., 2012).

Les mares peuvent être considérées comme des SNF car elles constituent de petits éléments aquatiques intégrés dans un paysage terrestre humide plus vaste, jouant un rôle disproportionné sur le plan écologique. Dans les tourbières, elles offrent un habitat pour des espèces aquatiques et semi-aquatiques souvent rares ou spécialisées, contribuent à la biodiversité locale, participent à la régulation hydrologique et favorisent des processus biogéochimiques spécifiques (Beadle et al., 2015). Leur petite taille et leur caractère parfois intermittent les rendent particulièrement vulnérables aux perturbations, même mineures, ce qui souligne l'importance de reconnaître leur valeur écologique (Calhoun et al., 2014; Boix et Batzer, 2016). Ainsi, les mares illustrent l'idée selon laquelle les écosystèmes fonctionnels ne dépendent pas de leur taille (Poschold et Braun-Reichert, 2017). Comprendre leur rôle permet d'apprécier les services écosystémiques qu'ils fournissent et d'orienter la conservation et la restauration des tourbières de manière plus efficace. Par leur

capacité à concentrer biodiversité, ressources et fonctions écologiques à petite échelle, les mares remplissent pleinement les critères qui définissent les SNF (Hunter, 2017; Hunter et al., 2017; Deák et al., 2021). Ces considérations motivent les objectifs de la présente recherche, qui vise à caractériser la végétation des mares, leur biodiversité et les facteurs environnementaux qui influencent leur colonisation spontanée dans les tourbières restaurées.

Objectif général et objectifs spécifiques

Dans l'introduction, plusieurs sujets clés ont été explorés, à savoir : (a) les impacts des activités anthropiques sur les tourbières; (b) l'importance des mares au niveau de la biodiversité et le besoin de les préserver; (c) la création des mares et les recherches sur leur revégétalisation; (d) le concept de « Small Natural Features ». Compte tenu des défis liés à la création de mares, l'objectif global de cette thèse est de mieux comprendre la diversité végétale associée aux mares dans les tourbières naturelles et restaurées, afin d'évaluer dans quelle mesure les pratiques de restauration écologique permettent de recréer ces habitats clés et de favoriser le retour des communautés végétales spécialisées. L'hypothèse centrale de cette recherche est que les mares se trouvant dans les tourbières restaurées présentent une diversité et une composition végétale différentes de celles des mares de référence, en raison de différences dans les conditions environnementales, ainsi que de choix de conception et d'aménagement qui peuvent ne pas reproduire pleinement les conditions naturelles. En conséquence, les objectifs spécifiques de cette thèse sont :

1. Déterminer les variables environnementales qui influencent l'établissement de la végétation typique des mares autour des mares créées, des canaux de drainage bloqués et des mares spontanées dans les tourbières ombrotrophes de l'est du Canada (Québec et Nouveau-Brunswick) (Chapitre 1).
2. Identifier la végétation associée aux mares en contexte de restauration écologique dans les tourbières minérotrophes, qu'elles soient créées volontairement ou spontanées, et déterminer les facteurs environnementaux influençant l'établissement de cette végétation, en évaluant également l'effet du contexte régional à travers une comparaison entre les mares de fen du Québec et du Manitoba (Chapitre 2).
3. Évaluer l'influence du gradient perpendiculaire autour des mares restaurées (créées et spontanées) dans des tourbières ombrotrophes sur la spécificité de la végétation, en comparaison avec les zones adjacentes hors mares dans l'est du Canada (Québec et Nouveau-Brunswick) (Chapitre 3).

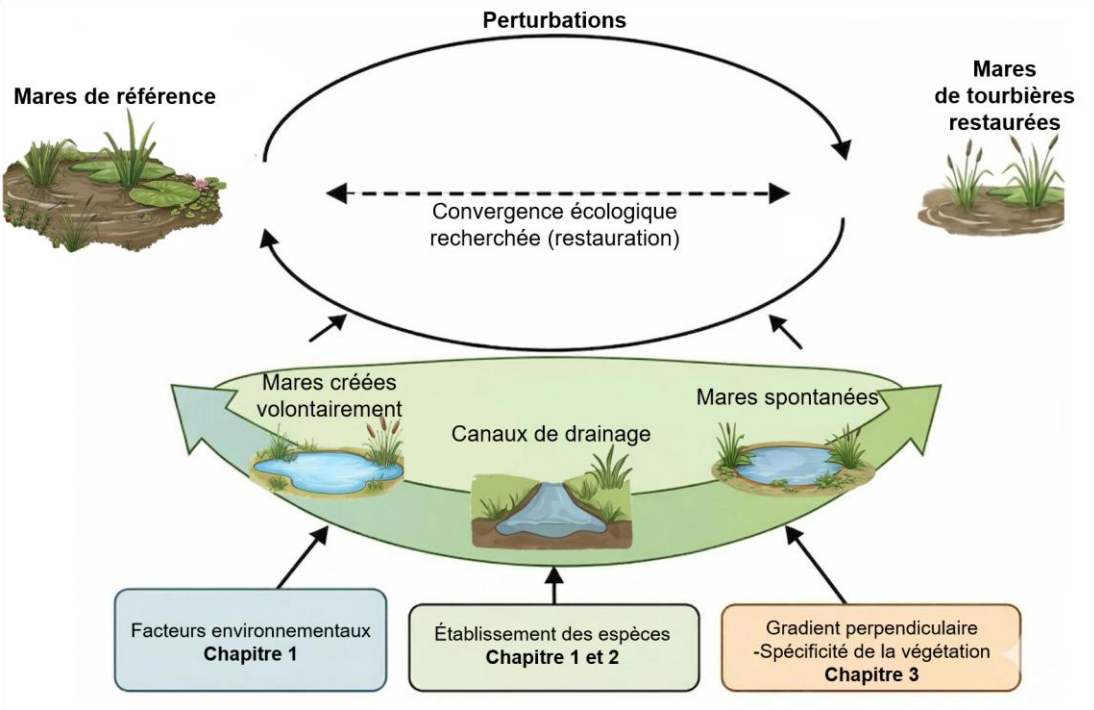

Figure 1. Cadre conceptuel pour comprendre les facteurs influençant l'établissement des espèces végétales typiques des mares dans une tourbière restaurée. L'ellipse du schéma formée par les lignes pleines représente le processus de restauration d'une mare qui a été perturbée. Ce processus de restauration est influencé par différents facteurs représentés par les encadrés reliés au schéma : les facteurs environnementaux, l'établissement des espèces végétales, ainsi que le gradient hydrologique perpendiculaire. Les facteurs environnementaux reflètent les conditions abiotiques de la mare après la restauration de la tourbière, telles que le pH, la chimie de l'eau, la morphologie de la mare, ainsi que le niveau et la stabilité de la nappe phréatique. Ces conditions représentent les contraintes auxquelles les espèces recolonisant la mare doivent faire face. L'établissement des espèces végétales fait référence à la capacité des plantes à s'établir et à persister dans ces conditions, en fonction de leurs caractéristiques écologiques et de leur tolérance aux conditions du milieu restauré. Le gradient perpendiculaire met en évidence l'influence de la connectivité entre la mare et son environnement immédiat. Ce gradient de connectivité peut affecter la disponibilité des propagules et influencer la composition des espèces qui colonisent la mare et ses abords. Ainsi, l'établissement des espèces végétales dans les mares des tourbières restaurées résulte de l'interaction entre les conditions environnementales et leur capacité à coloniser le milieu.

Chapitre 1 Environmental Influences on Plant Diversity in Restored and Natural Peatland Pools

1.1 Résumé

Les mares des tourbières sont des habitats essentiels pour la biodiversité, mais l'extraction de la tourbe élimine la végétation et assèche les sites, entraînant souvent la disparition des mares. Cette étude compare les conditions environnementales et la végétation de 59 mares issues de 14 tourbières à sphaignes restaurées (≥7 ans après restauration) à 26 mares de neuf tourbières de référence dans l'est du Canada. Trois types de mares restaurées ont été analysés : (1) mares créées, (2) mares spontanées et (3) canaux de drainage. Le type de mare explique 19 % de la variation de la composition floristique, tandis que la régionalité, la morphologie et la chimie de l'eau en expliquent 32 %. Les mares de référence sont homogènes et plus riches, tandis que les mares restaurées sont plus variables et moins diversifiées. Des mares plus profondes et la réintroduction d'espèces typiques favorisent la stabilité et la biodiversité.

1.2 Abstract

Peatland pools are crucial habitats for biodiversity, but peat extraction removes vegetation and drains sites, often eliminating pools. This study compared environmental conditions and vegetation in 59 pools from 14 restored *Sphagnum* peatlands (≥7 years post-restoration) with 26 pools from nine reference peatlands in Eastern Canada. We examined three restored pool types: (1) created pools, (2) spontaneous pools, and (3) open water in ditches. Pool type explained 19% of the variation in species composition, while regionality, morphology, and water chemistry accounted for 32%. Larger restored pools resembled reference pools morphologically and had higher dissolved organic carbon and nitrogen. Spontaneous pools exhibited elevated nitrogen (2.1 mg/L vs 0.57 mg/L) and phosphorus (0.08 mg/L vs 0.02 mg/L), and a higher pH that may favour non-target species, e.g., *Typha latifolia*. Reference pools had a uniform composition, comprising 20 associated species, whereas restored pools exhibited greater variability, reduced richness, and higher beta diversity. Post-restoration surveys emphasized the importance of deeper pools for water retention and chemical stability. Complementary measures, such as reintroducing typical pool species, are essential to ensure their establishment and enhance plant biodiversity in restored peatlands.

Keywords: aquatic plant species, biodiversity conservation, drainage ditches, ecological restoration, open water bodies, *Sphagnum*-dominated peatlands.

Introduction

Canada is the second country with the largest peatland area in the world, having a great responsibility for ensuring the protection of ecosystem services and biodiversity associated with these unique peat-accumulating ecosystems (UNEP, 2022). S*phagnum*-dominated peatlands in North America, or bogs, host unique plant communities due to their domed-shaped peat deposit that prevents connection with adjacent surface runoffs, limiting water input to precipitation and making the system acidic and impoverished in minerals (Payette and Rochefort, 2001). In addition, the peatland microtopography is often made up of a mosaic of microforms (small-scale structural elements, e.g., hummocks, hollows, and pools; Beadle et al., 2015; Couwenberg et al., 2022; Graham et al., 2020; Lindsay, 2010). Pools are considered biodiversity hotspots, as they concentrate assemblages of plants (Fontaine et al., 2007) and animal species (Mazerolle et al., 2006) that contrast with those found in the remaining surfaces within natural bogs. Since peatland pools foster diversity and abundance of specialized plants such as carnivorous plants, liverworts, pool *Sphagna*, and some aquatic species, they can be considered "small natural features" (Hunter et al., 2017). Therefore, they should be recognized as having ecological importance disproportionate to their abundance and extent in the landscape (Groves and Game, 2016; Hunter et al., 2017; Poschlod and Braun-Riechert, 2017).

Bog pools are distinguished by their unique morphological and chemical traits, which play a key role in determining the assemblages of colonizing plant and animal species (Beadle et al., 2015). Morphologically, pools in undisturbed bogs vary greatly in shape and size depending on climatic, topographical, and hydrological factors (Arsenault et al., 2022, 2019; Belyea and Lancaster, 2002). The pool morphology is characterized by a steep slope colonized by shrubby species such as Ericaceae and tree species, and a gentler slope dominated by herbaceous plants and mosses (Fontaine et al., 2007). For example, *Sphagnum* species, such as *S. cuspidatum*, along with liverwort carpets like *Cladopodiella* spp. and *Gymnocolea* spp., are characteristic of the boreal zone in North America (Fontaine et al., 2007; Poulin et al., 2002). Gentle edges often show very soft or even no slope at all and thus create homogeneous surfaces referred to as "wet lawns" (Payette and Rochefort, 2001).

The chemical properties that characterize peatland pools strongly influence the biodiversity and composition of plant and animal communities (Arsenault et al., 2019; Jolin et al., 2024; Mazerolle et al., 2006). Compared to pools present in marshes and swamps, bog pools present acidity conditions representative of adjacent surfaces (Kennedy and Mayer, 2002; Zoltai, 1987). As for dissolved organic carbon (DOC) and nitrogen concentrations in pools, they are mainly determined by internal processes related to pool depth, water temperature, and light penetration (Arsenault et al., 2018; Banaå, 2013; McEnroe et al., 2009; Moore et al., 2008; Pace and Prairie, 2005). From a hydrological point of view, pools are mainly fed by groundwater and precipitation, which also drive nutrient inputs (Payette and Rochefort, 2001). Water tables in reference pools

can fluctuate throughout the season, influenced by precipitation and evapotranspiration, but variations remain within the range of 10-30 cm (Dimauro and Hunter, 2002; Ferone and Devito, 2004; Holden et al., 2018; Quinton and Roulet, 1998).

Peat extraction dedicated to the horticultural market is a commercial activity affecting bogs, and although it does not take place over extensive areas at the country scale, it can significantly reduce bog areas regionally (Poulin et al., 2004) and lead to the destruction of bog pools. The ecological restoration of bogs aims to re-establish functional ecosystems that can support rich biodiversity and provide essential ecosystem services (González et al., 2014; Nugent et al., 2018). A substantial amount of effort has been carried out since the 1990s to develop an ecological restoration method for bogs, referred to as the "Moss Layer Transfer Technique" (MLTT) (Graf and Rochefort, 2016; Rochefort et al., 2003). In practice, the MLTT consists of reintroducing donor material, primarily Sphagnum fragments and companion bryophytes, onto the residual peat surface. This is combined with peat surface freshening, topographic modifications (e.g., berm creation for better water distribution), and the blocking of drainage ditches (Quinty and Rochefort, 2003; Rochefort et al., 2003). In conditions too harsh to allow a successful process based solely on spontaneous colonization, this restoration method enables the re-establishment of bog plants in around 5 to 10 years (González et al., 2014). Additionally, the MLTT helps restore hydrological conditions through rewetting practices, such as blocking drainage ditches (Landry and Rochefort, 2011). During restoration, former drainage ditches are blocked but not always filled with peat, allowing water to accumulate. This accumulation creates surfaces of open water and moisture gradients in the adjacent riparian zones, potentially favourable to the establishment of hydrophyte vegetation (Minkkinen and Laine, 2006). In this context, blocking drainage ditches leads to the formation of water bodies, hereafter called "pools". Additionally, water can accumulate in depressions created by machinery during restoration works or in the lowest areas of the terrain. Gradually, vegetation settles in, forming spontaneous pools (L. Rochefort, personal observations). Pools can also be created in restored peatlands following specific recommendations of Peatland Restoration Guide Quinty and Rochefort (2003): digging pools approximately 75 to 150 m² in size to ensure they are large enough to serve as wildlife habitats (Mazerolle et al., 2005), creating a depth of at least 1 to 2 meters to maintain water presence year-round, and the presence of a gentle slope on one side and a steep slope on the other to enhance habitat heterogeneity.

Despite efforts to replicate the morphology of reference pools, the created pools tended to have a more angular shape with predominantly steep edges, a consequence of excavation by machinery. Furthermore, the physical conditions of pools in restored peatlands can be very different from those in natural peatlands. Whittington and Price (2006) have thus demonstrated that the water table level is more variable in restored peatlands, implying variations in the water surface area of created pools, which can lead to temporary drying out. In response, vegetation colonization post-restoration varies (González and Rochefort, 2019), thus

affecting hydrological flows and nutrient cycling in pools (Arsenault et al., 2019). For example, *Sphagnum* mosses retain moisture and regulate the water table, even under drought (Brown et al., 2010), while decomposing plant matter, like nitrogen-rich larch leaves (*Larix* spp.), can release nutrients into the environment (Arsenault et al., 2019; Carlyle and Malcolm, 1986). Understanding how plant communities vary between pools with different physical and chemical properties can provide crucial insights into the processes shaping pool biodiversity and inform effective restoration strategies. However, the specific plant communities established around created and spontaneous pools, as well as blocked ditches, and their relationships with local and regional factors, remain poorly understood.

Research on pool margin revegetation in peatlands following the MLTT has progressed over time, addressing initial issues of the absence of plant recovery associated with pools, even six years after the overall restoration of a cut-over site (Fontaine et al., 2007). A subsequent study developed targeted techniques to assist the establishment of pool-typical plant communities, revealing that vascular plant germination is favoured by water levels close to the surface and by seedbeds of bare peat or formed of *Sphagnum* mat (Landry et al., 2012). To improve the success of pool restoration, research has highlighted the importance of simultaneously seeding vascular species while spreading bryophyte fragments and encouraging the introduction of *Sphagnum* mosses and liverworts such as *Odontoschisma fluitans* (Laberge et al., 2015). While these studies provide information on species composition or different techniques to be applied when restoring pools, there is a need for further knowledge of the environmental conditions that can influence the vegetation. Here, we sought to determine the environmental variables influencing the species diversity and composition associated with pools in restored bogs compared with pools in reference peatlands. To this end, we sampled reference pools, pools created during ecological restoration, spontaneous pools, and blocked drainage ditches, present in 23 peatlands in Eastern Canada (Quebec and New Brunswick), located in three climatic regions. Based on this scheme, we addressed the following research questions: (i) How do environmental conditions differ between the four types of pools; (ii) How do species diversity and composition vary between the four types of pools; (iii) Among spatial variables, the pool morphological and water chemistry variables, which environmental variables have the greatest influence on species diversity and composition?

Methodology

Study sites

This study was conducted in 85 pools distributed in 9 reference peatlands and 14 peatlands restored using the Moss Layer Transfer Technique (MLTT; for more details, see González and Rochefort, 2014) after horticultural peat extraction, located in the provinces of Quebec and New Brunswick, covering a range of 500 km east-west and 600 km north-south in Eastern Canada (Figure 2, Table 1.1). The locations of the studied

peatlands correspond to three Canadian climatic regions (Environment and Climate Change Canada, 2023): Atlantic Canada (n_{ref} = 6; n_{res}= 19), the Great Lakes/St. Lawrence Lowlands (n_{ref} = 9; n_{res}= 26), and the Northeastern Forest (n_{ref} = 11; n_{res}= 14) (Table 1.1). Atlantic Canada experiences a maritime climate, influenced by the Atlantic Ocean, which brings cooler summers and milder winters with less snow cover. The mean annual air temperature is 4.8°C, with a total yearly precipitation of 1,110 mm and a growing season lasting 133 days (climate normal for Miramichi station; Environment and Climate Change Canada, 2023). In contrast, the Great Lakes region experiences a continental climate with warm summers and cold winters, a mean annual air temperature of 3.2°C, total annual precipitation of 1,000 mm, and a growing season of 150 days. In the Northeastern Forest region, the mean annual air temperature is 3.4°C, total annual precipitation is 998 mm, and the growing season lasts 137 days. This weather information is based on climate normal from 1981 to 2010 (Environment and Climate Change Canada, 2023).

The reference peatlands in this study were ombrotrophic (i.e., bogs) and were characterized by the dominance of *Sphagnum* mosses and ericaceous shrubs (Zoltai and Vitt, 1995). The restored peatlands were ombrotrophic, with an average residual peat depth of 121 cm (standard deviation [SD] = 62.3), showing an average pH of 3.7 (SD = 0.4) and an electrical conductivity of 111 µS/cm (SD = 101.4). These data were collected from the large-scale monitoring database of the Peatland Ecology Research Group (PERG).

The surface of each peatland was examined using satellite images from Google Earth to visually detect the presence of pools. The reference pools were selected to ensure a wide diversity of shapes by choosing pools of large, medium, and small sizes. A minimum of 3 and a maximum of 6 pools were selected per site to represent the variability in size (surface area) at each site, while depth was subsequently measured in the field. In total, 26 reference pools and 59 restored pools were identified and surveyed. In restored peatlands, we considered the following habitats as pools: intentionally created pools for ecological restoration purposes (n = 19), spontaneous pools formed after the passage of heavy machinery or formed in wetter areas (n = 27), and shallow drainage ditches that have been blocked to raise the water table (n = 13). To be selected, pools within restored peatlands needed to meet these two additional criteria: are located in a bog with a minimum of 7 years post-restoration (the sites sampled have an age range between 11 and 29 years post-restoration), showing a successful re-establishment of a peatland plant community, with an average vegetation cover of 40% dominated by *Sphagnum* and true mosses (González et al., 2014). The MLTT was theoretically applied uniformly in all the restored sectors (González and Rochefort, 2014), but because of potential logistical constraints (e.g., areas too wet for machinery), the transfer of the moss layer exhibited probable heterogeneity. Additionally, none of the pools within restored peatlands had undergone specific management regarding the seeding of vegetation. As a result, the vegetation colonization could have reflected both contributions from

the MLTT and spontaneous colonization, influenced by local factors such as the proximity of other restored sectors, natural peatlands, and areas with human activities (e.g., agriculture, grazing).

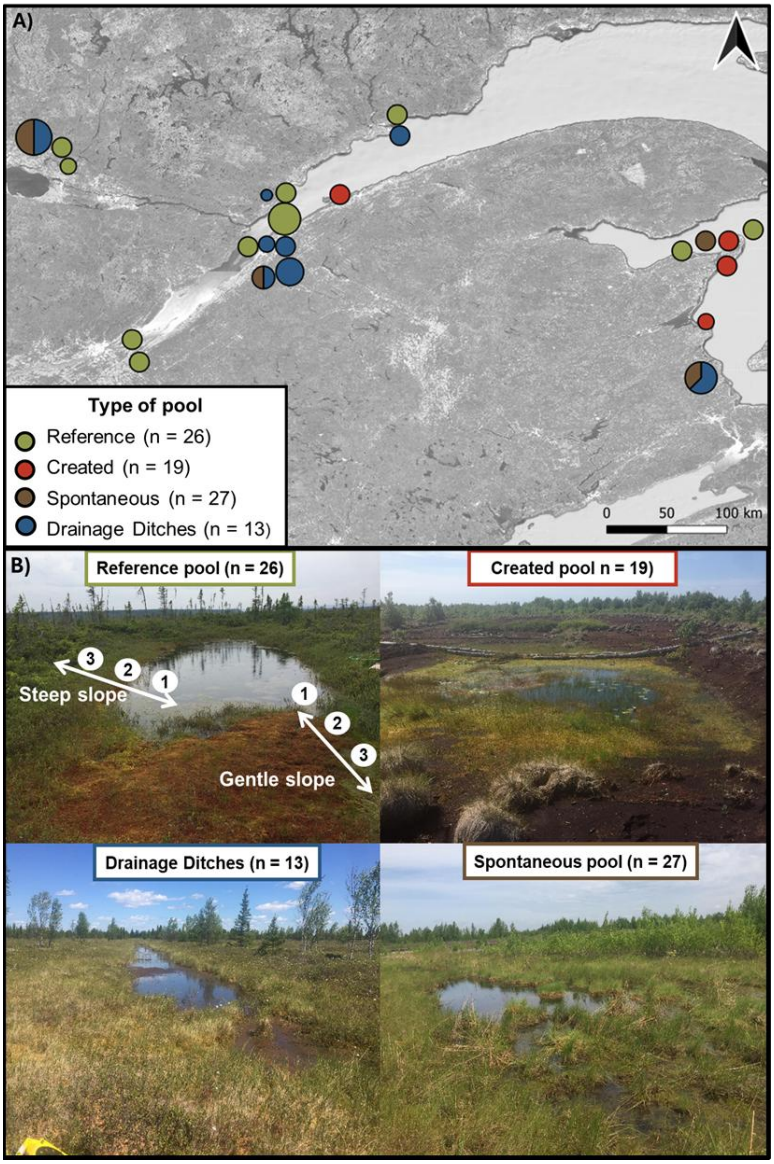

Figure 2. A) Location of the 85 surveyed pools located on 23 peatlands (9 reference peatlands and 14 restored peatlands) in the provinces of Quebec and New Brunswick (Eastern Canada) B) Pool types and sampling method illustrating the location of transects and quadrats (Q1 = directly in the water right at the pool edge, Q2 = right outside the pool at the edge, and Q3 = 2 m away from the edge). The larger points in sub-figure A represent a greater number of associated pools. This map was created using ArcGIS Desktop 10.8.2., sourced from OpenStreetMap contributors. Map projection: Lambert Conformal Conic (NAD83(CSRS) / Canada Lambert, EPSG:3978). Credit for the photos: Laura Catalina Riaño Peña.

Vegetation surveys

The pools were surveyed using four transects positioned perpendicular to the pool margin, with two located on the gentle slope and two on the steep slope (Figure 2), during the summer of 2021 (June to August). This

approach was applied primarily to natural pools (n = 26) and created pools (n = 19). In contrast, drainage ditches, which are sometimes reprofiled, and spontaneous pools, which tend to form with minimal inclination, generally exhibit only gentle slopes. In these cases, all four transects were sampled regardless, typically representing a single slope type (n = 36 pools), while some drainage ditches included both slope types (n = 4). Early in the study, we conducted preliminary analyses to evaluate the potential influence of slope; however, the results were inconclusive due to the lack of consistent slope types across the pools. On each transect, three one-meter-diameter quadrats were surveyed. The first quadrat was placed directly in the water at the pool edge, the second quadrat was positioned right outside the standing water at the edge, and the third was set 2 m away from the edge (Figure 2). In each quadrat (n = 1.020), the cover of the following strata was assessed: ericaceous shrubs, other shrubs, herbaceous plants, and mosses (including sphagnum mosses, liverworts, and other mosses), with identification down to the species level, to the most accurate percentage of cover possible, and as an estimation of their vertical projection on the ground. Unidentified plant species were collected in the field and identified in the laboratory. Nomenclature follows the *Flore des bryophytes du Québec-Labrador* (Faubert, 2012) for bryophytes, *Sphagnum Mosses of Eastern Canada* (Ayotte and Rochefort, 2020) for *Sphagnum* and *Flora of North America* (Morin, 2000) and VASCAN, the Database of Vascular Plants of Canada (Brouillet et al., 2010) for vascular species.

Vegetation classification

To study the effect of environmental conditions related to pools on plant communities, diversity, and composition, a systematic classification of vegetation, including both bryophyte and vascular plant species, was undertaken. Based on a thorough review of the literature (Faubert, 2012; Lachance et al., 2021; Lemmer et al., 2023; Morin, 2000; Payette and Rochefort, 2001; Vitt, 2014), all plants species were grouped into three distinct and exclusive categories according to their habitat characteristics (see Fig. 1.1 for the decisional tree and Table 1.2 for species classification):

1. Species preferring open-water pools of *Sphagnum*-dominated peatlands (POOL): this category comprises ombrotrophic peatland species that are occasionally, frequently, or preferentially present on the edges of or within pools of undisturbed reference peatlands.
2. Species preferring *Sphagnum*-dominated peatlands microforms, other than pools (BOG): This category includes ombrotrophic peatland species found in microforms other than pools within peatlands, such as hummocks, spruce thickets, and laggs, and that are rare or absent from the pools or the edges of pools of undisturbed reference *Sphagnum*-dominated peatlands.
3. Species preferring other habitats than *Sphagnum*-dominated peatlands (OTHER): This category includes all species absent or rare in reference peatlands, with species commonly found in lowland habitats, alongside species typically found in various types of wetlands.

Environmental conditions

Environmental variations at each pool were characterized by measuring several parameters. The coordinates of each pool (i.e., latitude and longitude) were recorded with a GPS tablet using an offline mapping application Avenza Maps (5-10 m of spatial precision). The perimeter and surface area of pools were assessed using satellite imagery sourced from Google Earth in winter 2021. The presence of ice on the surface of the pools has made it possible to obtain a more precise view of their extent using satellite photography. The depth of pools was measured using a 4-meter string attached to a disk, ensuring minimal disruption to the pool bed, comprised of unconsolidated sediments. The depth of peat deposits in peatlands was assessed in the vicinity of each pool by inserting a metal rod into the peat until mineral soil was reached. To characterize the chemical properties of the pools, in-water measurements were taken. The pH was directly assessed in the field (one measurement per pool) using a pH meter (HI98129, Hanna Instruments). One water sample was collected per pool for chemical composition analysis, including dissolved organic carbon (DOC), total nitrogen (N_{total}), and total phosphorus (P_{total}). All samples were frozen until the analytical procedures were carried out. Total phosphorus and total nitrogen were analyzed following the Qualls (1989) method. For the analysis of dissolved organic carbon (DOC), the water sample was acidified to a pH between 2 and 4 and sparged with the carrier for five minutes. This step aimed to remove carbonates and bicarbonates, components of inorganic carbon, thereby determining the non-particulate organic carbon (NPOC) content. Subsequently, the sample was vaporized using a Shimadzu TOCVcsn/MTN-1 analyzer (Shimadzu, Kyoto, Japan), and the resulting CO_2 was quantified using an IRGA (Infra Red Gas Analyzer), with results expressed in milligrams of dissolved organic carbon per liter (mg DOC/L).

Statistical analysis

How do environmental conditions differ between the four types of pools?

The independent variables measured to characterize the environmental conditions of pools were of three types: regionality (latitude and longitude), pool morphology (perimeter, surface area, pool depth, and peat depth), and chemistry of the water (pH, total nitrogen, total phosphorus, and DOC) (see Fig. 1.2 for the correlation matrix). Before conducting analyses, all continuous environmental variables were standardized (Oksanen and Simpson, 2009). The type of pool was treated as a four-level factor: reference, created, spontaneous, and drainage ditches. Differences in environmental conditions across pool types were tested using one-way ANOVAs and Tukey's HSD tests for pairwise comparisons (Abdi and Williams, 2010) using the stats R package.

How do species diversity and composition vary between the four types of pools?

The dependent variables corresponded to the vegetation data, expressed as plant mean abundance (cover) and species richness, i.e., plot-scale data were averaged at the pool scale (n = 85). Specifically, the analyses aimed to explain variations in the cover and richness of all plant species (TOTAL), in the cover and richness of species preferring pools (POOL), and those preferring other *Sphagnum*-dominated peatland microforms (BOG), independently. As the OTHER category was represented by too few species, it was not statistically tested. Differences in the cover and richness of total species (TOTAL), pool-preferring species (POOL), and other peatland microform species (BOG) across pool types were tested using one-way ANOVAs and Tukey's HSD tests for pairwise comparisons. Furthermore, differences in species composition among the four pool types were assessed using a PERMANOVA analysis (vegan R package, Oksanen et al., 2024) with 999 permutations (Anderson and Walsh, 2013), followed by pairwise comparisons (Martinez Arbizu, 2020). In addition, a PERMDISP analysis (vegan R package, Oksanen et al., 2024), also with 999 permutations, was conducted to test for differences in the variability (dispersion) of species composition among pool types. These analyses were based on a Hellinger distance matrix using the mean cover of species in each pool. Finally, we used the *phi* coefficient of association (indicspecies R-package, De Cáceres and Legendre, 2009) to investigate individual species associations with each type of pool and test the statistical significance of the associations using permutation tests (n = 999).

Which environmental variables have the greatest influence on species diversity and composition?

To assess whether changes in environmental conditions influenced the cover (log-normal distribution) and richness (Poisson distribution) of plant species (TOTAL, POOL, BOG), mixed-effects linear and generalized linear models were used (lme4 R-package; Bates et al., 2015). We considered a set of 10 *a priori* models, plus a null model, to independently test the effect of regionality (n = 2), morphology (n = 4 variables), and chemistry (n = 4) variables on the cover and richness of the three categories of plant species (TOTAL, POOL, BOG). Since the pools within each peatland were not independent, we used peatland (n = 23) as a random effect. Variance explained by models was determined by using the marginal coefficient of determination for fixed effect parameters alone (Nakagawa et al., 2017). We used the Akaike Information Criterion corrected for small sample sizes (AICc) to rank the models, with particular attention to models that had AICc weights greater than 0.95, indicating strong support compared to other models. For each response variable, we extracted the parameter estimates and associated unconditional standard errors to determine the significance and the relative magnitude of the effect of each environmental parameter (MuMin R-package, Barton, 2015). Finally, we used a distance-based redundancy analysis (db-RDA) on a Hellinger distance matrix (vegan

package) with 999 permutations to determine how variations in environmental parameters explained changes in species composition.

All analyses were performed using R Studio (R Core Team 2022, version 4.2.2) software.

Results

Variations in environmental conditions across pools

Regarding pool morphology, reference pools were significantly deeper (mean = 106 cm) than all three other types of restored pools (created = 57.6 cm; spontaneous = 25.3 cm; ditches = 47.1 cm) (Table 1 and Table 1.3 for details of pairwise comparisons). Drainage ditches were characterized by a large perimeter (346 m) compared to all other pools, even in comparison with reference pools (95 m). Reference pools were larger in surface area (673 m^2) than created (133 m^2) and spontaneous pools (94 m^2), but comparable to the area of ditches (427 m^2). Mean depth of the surrounding peat deposit was significantly thicker for the reference pools (299 cm) compared to the other pools (created = 159 cm; spontaneous = 106 cm; ditches = 122 cm). Additionally, the mean depth of peat deposits near the pools was higher for created pools (159 cm) compared to spontaneous pools (106 cm).

DOC was higher in pools of managed peatlands (created = 52 ± 24 mg/L; spontaneous = 70 ± 31 mg/L; ditches = 60 ± 29 mg/L) compared to reference pools (22 ± 9 mg/L). A similar pattern emerged for total nitrogen (N_{total}) concentrations, where reference pools have lower values (0.57 ± 0.17 mg/L) than those within restored peatlands (created = 1.2 ± 0.5 mg/L; spontaneous = 2.1 mg/L ± 0.8; ditches = 2.2 ± 1.1 mg/L). In addition, created pools had higher values of total nitrogen than ditches and spontaneous pools. Finally, total phosphorus concentrations (P_{total}) showed higher values for spontaneous pools only (0.08 ± 0.1 mg/L) when compared to reference pools (0.02 ± 0.02 mg/L).

Table 1. Variations in spatial, morphological, and chemical conditions (mean ± standard deviation [SD]) between the four types of pools in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick). Different letters indicate a significant difference between the type of pools (One-way ANOVA + Pairwise comparison Tukey HSD; Appendix 1.3), the alpha level was 0.05.

Groups	Variables	Reference pools		Restored pools						F-value	p-value
				Created pools		Spontaneous pools		Drainage ditches			
Spatial	Longitude (Long; °)	47.98 (±0.83)		47.85 (±0.36)		47.89 (±0.92)		47.85 (±0.99)		0.1	0.949
	Latitude (Lati; °)	69.09 (±2.59)		67.41 (±2.25)		69.03 (±2.24)		68.50 (±3.42)		1.9	0.128
Morphology	Pool perimeter (Perimeter; m)	95 (±90)	a	44 (±13)	a	42 (±64)	a	346 (±104)	b	56.7	**< 0.0001**
	Pool area (Area; m^2)	672 (±1091)	a	133 (±68)	b	94 (±167)	b	427 (±231)	ab	4.6	**0.005**
	Pool depth (Depth; cm)	106 (±66)	a	57 (±40)	b	25 (±13)	b	47 (±23)	b	15.8	**< 0.0001**
	Peat depth (Peat_depth; cm)	299 (±24)	a	159 (±79)	b	106 (±48)	c	121 (±51)	bc	69.4	**< 0.0001**
Chemical	pH	3.41 (±0.46)		3.86 (±0.60)		3.66 (±0.77)		3.78 (±0.67)		2	0.109
	Total phosphorus (P_{total}; mg/L)	0.02 (±0.02)	a	0.04 (±0.03)	ab	0.08 (±0.10)	b	0.06 (±0.07)	ab	4.6	**0.005**
	Total nitrogen (N_{total}; mg/L)	0.57 (±0.17)	a	1.19 (±0.46)	b	2.10 (±0.83)	c	2.25 (±1.14)	c	29.2	**< 0.0001**
	Dissolved organic carbon (DOC; mg/L)	21.94 (±8.90)	a	52.10 (±23.99)	b	69.76 (±30.74)	b	60.11 (±28.59)	b	18.7	**< 0.0001**

Variations in plant diversity and species composition across pool types

Total species richness (TOTAL) was higher in reference pools (mean ± standard deviation [SD] = 28 ± 3 species) compared to spontaneous pools (19 ± 6). Although created pools (26 ± 10) had higher total species richness compared to spontaneous pools. The richness of species classified as typical of pools (POOL) was higher in reference pools (9 ± 1) compared to created pools (6 ± 1), spontaneous pools (5 ± 1), and ditches (6 ± 2) (Table 2). Finally, the richness in species belonging to other bog microforms (BOG) was lower in spontaneous pools (11 ± 4) compared to each of the three other types of pool (Table 2).

For total species cover (TOTAL), created pools had lower values (mean ± standard deviation [SD] = 24 ± 11%) than the other pools. For the cover of POOL specialized species, no significant differences were found between the four pool types. Finally, the cover of species associated with other bog microforms (BOG) was higher in reference pools (30 ± 7%) compared to created pools (7 ± 6%) and spontaneous pools (13 ± 15%), but comparable to ditches (Table 2 and Table 1.4, and Table 1.5 for details).

The PERMANOVA analysis ($F_{3,81}$ = 6.52, R^2 = 19.47%, p = 0.001) showed that species composition varied significantly between the different restored pool types (Figure 3); pairwise comparisons showed that the species composition was significantly different among all pairs of pools (Table 1.6). Furthermore, the PERMDISP analysis ($F_{3,81}$ = 13.52, p < 0.001) also revealed a significant difference in the degree of site dispersion around centroids (i.e., the average distance to the centroid [Reference = 0.5266, Created = 0.7012, Ditches = 0.6754, Spontaneous = 0.7776]) (Table 1.7). The pairwise comparison exhibited significant differences between reference pools and all three types of pools within restored peatlands. This indicated greater differences in species composition within created, spontaneous, and ditches compared to reference pool sites.

The *phi* coefficient of association (Table 1.8) revealed that 20 species were significantly associated with reference pools, including *Drosera rotundifolia, Kalmia polifolia, Rhynchospora alba, Sarracenia purpurea* and *Sphagnum fuscum*; five species were significantly associated with created pools, including, *Hypericum fraseri*, *Typha latifolia, Vaccinium macrocarpon*; three species were significantly associated with spontaneous pools, i.e., *Eriophorum vaginatum, Scirpus cyperinus* and *Sphagnum fallax*; six species were significantly associated with drainage ditches, i.e., *Larix laricina*, *Rhododendron groenlandicum, Sphagnum flavicomans*, *Sphagnum majus, Sphagnum russowii,* and *Vaccinium angustifolium.*

Table 2. Habitat-specific species richness and total cover (mean ± standard deviation [SD]) between the different types of pools in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick). Habitat-specific categories are represented with the cover and richness of total species (TOTAL), species typical of other bog microforms (BOG) and bog pool species (POOL). Different letters indicate a significant difference between the four types of pools (One-way ANOVA + Pairwise comparison Tukey HSD; Appendix 1.5); the alpha level was 0.05.

						Restored Pools					
		Reference pools		Created pools		Spontaneous pools		Drainage ditches			
	Variable	**Mean** (±SD)		**Mean** (±SD)		**Mean** (±SD)		**Mean** (±SD)		**F-value**	**p-value**
Richness	**TOTAL**	28 (±3)	a	26 (±10)	a	19 (±6)	bc	23 (±4)	ac	8.4	**<0.0001**
	POOL	9 (±1)	a	6 (±1)	b	5 (±1)	b	6 (±2)	b	31.9	**<0.0001**
	BOG	17 (±2)	a	15 (±6)	a	11 (±4)	b	16 (±2)	a	8.5	**<0.0001**
Cover	**TOTAL**	54 (±10)	a	24 (±11)	b	45 (±25)	a	47 (±24)	a	9.8	**<0.0001**
	POOL	23 (±11)		15 (±12)		30 (±22)		24 (±20)		2.6	0.057
	BOG	30 (±7)	a	7 (±6)	b	13 (±15)	bc	21 (±14)	ac	16.2	**<0.0001**

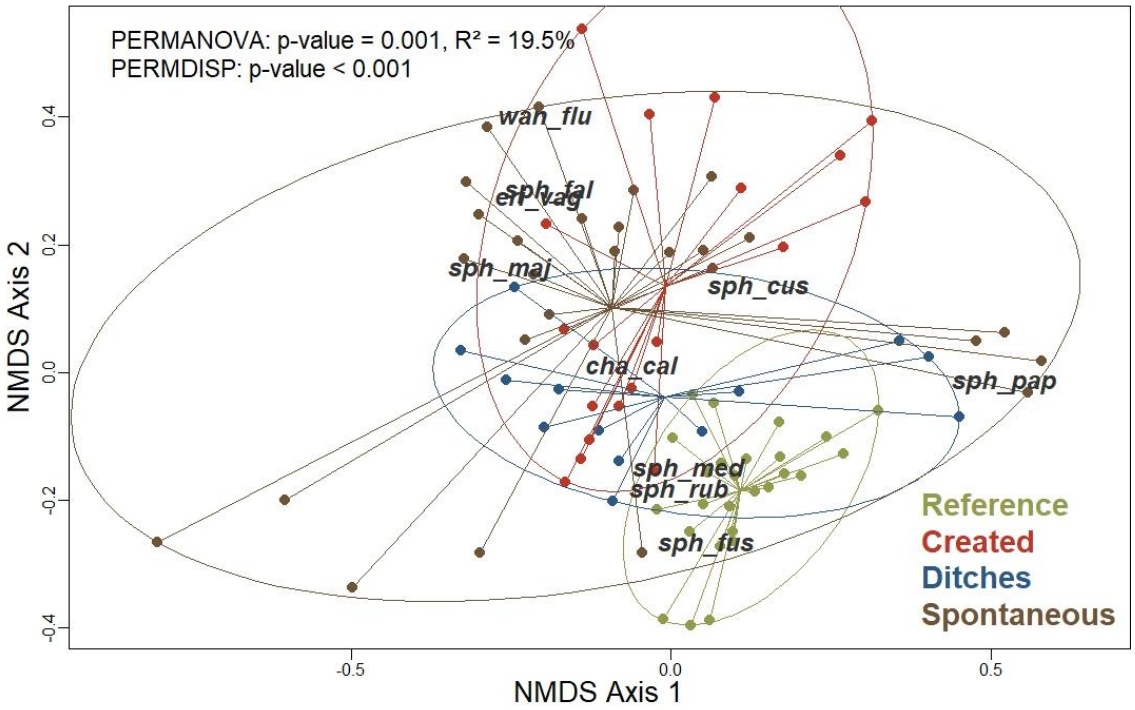

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination plot of the Hellinger distance matrix, making a distinction between the plant species composition in the four types of pools in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick, Appendix 1.3). Furthermore, the scores of the 10 most abundant species are shown (*cha_cal = Chamaedaphne calyculata, eri_vag = Eriophorum vaginatum, sph_cus = Sphagnum cuspidatum, sph_fal = Sphagnum fallax, sph_fus = Sphagnum fuscum*, *sph_maj = Sphagnum majus, sph_med = Sphagnum medium, sph_pap = Sphagnum papillosum, sph_rub = Sphagnum rubellum, wan_flu = Warnstorfia fluitans).* Species are displayed via the position of the species labels (see Appendix 1.6 and 1.7 for more details).

Effects of environmental conditions on species diversity and composition

Among the mixed-effect models testing the influence of individual environmental conditions on variations in plant species richness and cover, only one top-ranked model had an AICc weight (W, Table 3) greater than 0.95, indicating strong support relative to other models. The perimeter of the pool best explained variations in TOTAL species and BOG species richness, while the depth of the surrounding peat best explained variations in the richness of POOL species. In addition, DOC concentrations best explained variations in TOTAL species cover, pH explained variations in POOL species cover, and the depth of the surrounding peat best explained variations in BOG species cover. The goodness of fit (R^2, Table 3) of these top-ranked models ranged from 4.7% for POOL species cover to 32.4% for POOL species richness. Furthermore, the consistent absence of the null model among the top-ranked models underscores the importance of environmental parameters in explaining variations in plant richness and cover (see Table 1.9 for detailed results).

Regarding the significance of each variable, i.e., those whose confidence intervals did not include zero (Figure 4; Table 1.4), our results revealed that species richness in TOTAL, POOL, and BOG groups significantly

increased with both peat and pool depth. In contrast, POOL species richness significantly declined with increasing concentrations of total phosphorus (P_{total}), total nitrogen (N_{total}), and dissolved organic carbon (DOC). Pool morphology, specifically larger perimeter and area was associated with greater BOG and TOTAL species richness, while higher pH levels increased TOTAL species richness only. For species cover, pool location (longitude and latitude), pool depth, and surrounding peat depth all contributed to increased BOG species cover. Surrounding peat depth also enhanced the TOTAL species cover. Conversely, higher DOC concentrations and elevated pH reduced TOTAL species cover, and high pH levels further decreased POOL species cover.

The db-RDA showed that 32.3% ($F = 5.01$, $p = 0.001$) of the variation in species composition was explained by measured environmental variables (Figure 5, Table 1.10). Among the 10 variables tested, 9 significantly explained variations in species composition (i.e., excluding phosphorus concentration). The longitude explained 24% ($p = 0.001$) of the constrained inertia, the depth of surrounding peat deposit 22.2% ($p = 0.001$), the pH 8.5% ($p = 0.002$), the concentration of dissolved organic carbon (DOC) 8.1% ($p = 0.003$), the latitude 7.4% ($p = 0.002$), the nitrogen concentration 7.4% ($p = 0.003$), the perimeter 7.1% ($p = 0.005$) and the area 6.6% of the pool ($p = 0.01$).

Discussion

Peatland pools are vulnerable to land-use disturbances. Preserving the biodiversity and ecological functions of natural pools, while promoting their recovery in restored peatlands, requires a better understanding of the environmental conditions that support these habitats (Beadle et al., 2015). In this study, through a sampling plan comparing the vegetation of four types of pools (reference, created during peatland restoration, spontaneously formed, and generated after ditch blocking) with different environmental conditions, we have shown a clear difference in the species diversity and composition between the reference pools and the pools within restored peatlands. Our results showed that the environmental conditions of pools in restored peatlands did not resemble those of reference pools in natural peatlands. For example, elevated concentrations of nitrogen, phosphorus, and dissolved organic carbon (DOC) at restored sites reduced the richness of species typically found in reference pools. This suggests that it was not only the morphological characteristics of the pools that were associated with poorer plant communities, but also the chemical composition of the pool water.

The environmental conditions of reference peatland pools differed from those of restored peatland pools

Restoration as practised following the MLTT principles (Quinty et al., 2019, 2020a, b, c) does not enable the creation of pools with morphological properties close to those existing under natural conditions (Arsenault et al., 2019). Reference pools differed from pools within restored peatlands not only in surface area, which can vary from 100,000 m² to less than 10 m², but also in depth, which is often more than 1 m (Arsenault et al., 2022;

Belyea and Lancaster, 2002). In our sampling area, the morphology of restored pools was highly heterogeneous. For example, spontaneous pools were typically small and shallow. Field observations by the first author indicated that water persistence in these pools was generally temporary, varying with weather conditions. They often held water in spring but tended to dry out during the summer. This pattern is consistent with all pools found in ecological restoration sites. In contrast, the created pools tended to be more square-shaped and shallower than the reference pools, although they were still deeper than spontaneous pools. Drainage ditches, on the other hand, were characterized by their large perimeter and linear, artificial shape within the landscape. Interestingly, they were the only structures that matched the reference pools in terms of surface area.

According to Arsenault et al. (2018), the morphological characteristics of the pools likely contributed to the significant variations in water chemistry observed in our study. For instance, the temporary presence of water in restored pools can enhance aerobic decomposition due to a lowered water table (Armstrong et al., 2009). As a result, the oxygenation of the exposed peat substrate accelerates the breakdown of organic matter, leading to mineralization and the subsequent release of previously immobilized nitrogen and phosphorus into the water (Holden et al., 2006) as well as increased production of dissolved organic carbon (DOC) (Clymo, 1984). Unfortunately, we did not measure seasonal water table fluctuations in each pool, which limits our ability to directly assess the influence of water presence or absence on these processes within pools. The large surface area of drainage ditches provides an extensive edge surface, surpassing that of other pools within restored peatlands. This generates a larger water-peat interface, which may facilitate the decomposition of organic matter and lead to increased concentrations of N, P, and DOC in the stagnant water of the ditches (Armstrong et al., 2009; Holden et al., 2006). Also, in some cases, mineral soil can be reached when ditches are dug, with a higher minerogenic influence in the water (Haapalehto et al., 2014; Little-Devito, 2024). Generally, the shallowness pools within restored peatlands were associated with higher dissolved organic carbon (DOC) concentrations, total nitrogen, and phosphorus. Total phosphorus and nitrogen concentration values in pools have been linked to the relationship between higher temperature conditions and shallower depths, which simultaneously generate increased microbial activity at the peat-water interface, resulting in greater decomposition (Arsenault et al., 2024; Moore et al., 2008; Pace and Prairie, 2005).

Water chemistry can be influenced not only by pool morphology but also by the surrounding vegetation, which interacts with morphological features such as pool depth (Arsenault et al., 2019, 2018; Prijac et al., 2022; Turner et al., 2016). Tree species around pools, such as *Larix laricina*, can increase total nitrogen concentration by improving mineralization and nitrogen availability in peatlands due to needle litter deposits (Arsenault et al., 2019; Carlyle and Malcolm, 1986). In the case of drainage ditches, our results showed high concentrations of total nitrogen, often associated with the presence of trees persisting due to the historical impact of drainage. The greater fluctuation of the water table in restored peatlands favours the colonization of trees, e.g., *Larix laricina*

(González and Rochefort, 2014; Haapalehto et al., 2011), explaining its strong association with ditches, as confirmed by the *phi* coefficient (see Table 1.8 for more details).

Table 3. Top-ranking models predicting variations in plant species cover and richness according to their preferential habitat in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick). Akaike's information criterion corrected for small sample sizes (AICc) was used. The number of estimated parameters (k), AICc, AICc weight (W), and adjusted coefficient of determination (R^2) were provided (see Appendix 1.9 for detailed results of all candidate models). Habitat-specific categories were represented by the cover and richness of total species (TOTAL), bog pool species (POOL), and species typical of other bog microforms (BOG).

	Variables	Candidate model	k	AICc	W	R^2
Richness	TOTAL	Perimeter	3	556.8	0.319	0.063
	POOL	Peat depth	3	365.7	0.997	0.324
	BOG	Perimeter	3	497.9	0.366	0.082
Cover	TOTAL	DOC	4	143.1	0.537	0.136
	POOL	pH	4	222.1	0.330	0.047
	BOG	Peat depth	4	201.9	0.511	0.158

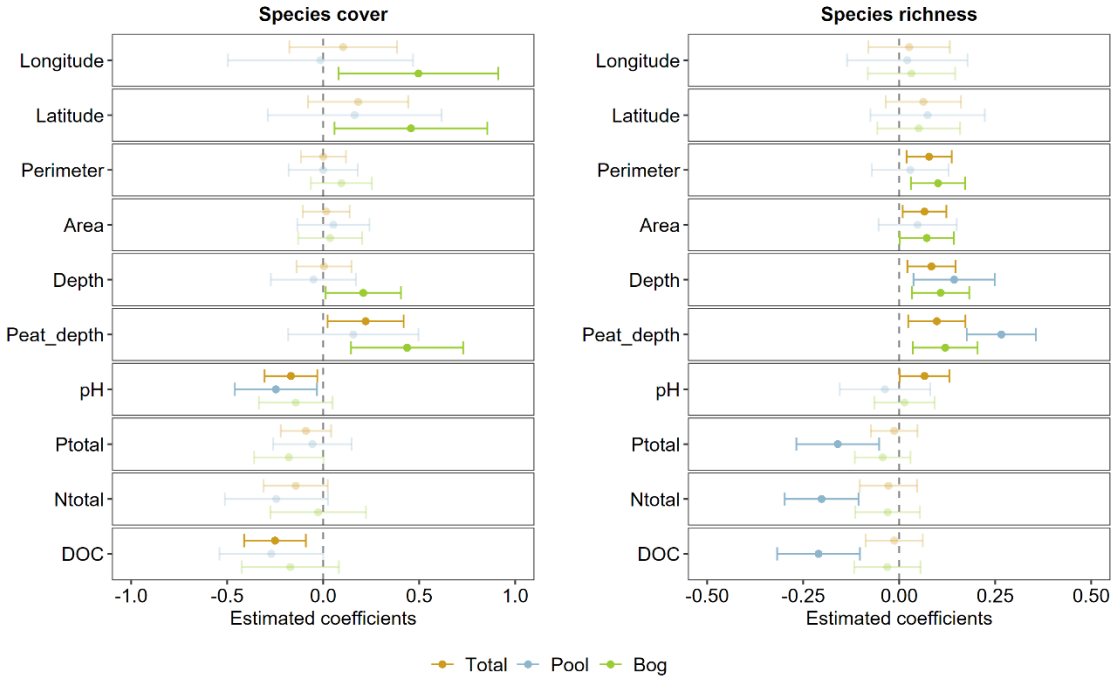

Figure 4. Average parameters estimate and 95% confidence intervals for environmental parameters used to predict variations in habitat-specific species richness and cover within the four types of pools in Eastern Canada (Quebec and New Brunswick provinces; Appendix 1.4). Habitat-specific categories are represented by the richness and cover of total species (TOTAL), typical pool species (POOL), and species typical of other bog microforms (BOG).

How do species diversity and composition vary across pools?

As expected, and partly due to the large differences in the morphology and water chemistry between the four types of pools, significant differences in species diversity were highlighted. Indeed, plant species richness was greater in reference pools than in spontaneous pools for all plant categories (TOTAL, POOL, BOG), and reference pools had the highest richness of pool-typical species compared to all other pools within restored peatlands (i.e., created, spontaneous, and ditches). Regarding plant cover, the main differences were found when comparing created pools, which had lower overall vegetation cover, with other pool types, both for total richness and for species typical of other bog microforms. This pattern may be related to the way the created pools were engineered, with more pronounced edges despite efforts to design them with softer margins. Considering that no active reintroduction of pool-specific plants was realized, and the same restoration technique of MLTT was theoretically applied uniformly to the inventoried sites (González and Rochefort, 2014), our results suggested that it was possible to naturally regenerate a vegetation cover, but not its diversity, in recreated pools. Indeed, according to Fontaine et al. (2007), even six years after applying the MLTT, species typical of pools were not recolonizing the pools that had been created. In pools within restored peatlands, water levels fluctuated more significantly than in reference pools, exhibiting sharper increases and more rapid recessions of water (Holden et al., 2018). Due to the absence of hydrological connections between pools (essential for hydrochory) in ecological restoration (field observation), a vegetation reintroduction technique may be required to accelerate the establishment of characteristic pool vegetation.

In terms of the creation of pools, the method used so far involved digging the pools with a mechanical shovel, resulting in a rather square pool morphology characterized by very steep edges (Quinty and Rochefort, 2003). In this way, the morphological characteristics of the created pools could act as an ecological filter, limiting plant establishment or creating new niches unsuitable for species typical of pools and even for those characteristics of bogs. For example, species strongly associated with the created pools were not necessarily typical of bog species, e.g., *Typha latifolia*. This species is highly competitive, forming monotypic stands in shallow open water areas (Grace and Wetzel, 1981), which reduces vegetation diversity by competition (Drexler and Bedford, 2002; Fontaine et al., 2007; McNaughton, 1968).

In natural bogs, pools are often found in open areas characterized by vegetation composed of liverworts and *Sphagnum* species, mainly from the *Subsecunda* and *Cuspidata* subgenera. These species are complemented by vascular species adapted to these microforms (Fontaine et al., 2007). After the restoration process, peatlands (and pools) can exhibit changes in species composition (Johansen et al., 2017). Our results revealed significant differences in species composition among the types of pools studied. Reference pools exhibited more homogeneous species composition, with more shared plant species across the different sampled reference pools. In contrast, pools within restored peatlands showed the opposite trend. For example, spontaneous pools

exhibited the largest dispersion values, indicating high turnover in species identity between pools. Created pools and drainage ditches also displayed notable dispersion in species composition between sites, although less pronounced than spontaneous pools. Overall, pools within restored peatlands exhibited significant variability in species composition, both between different pools and within the same type of pool. This led to a decrease in species uniqueness (richness) compared to reference pools, as well as considerable variation in species composition within the same type of pool. This trend toward changes in plant composition within a restored environment can be attributed to several factors, including the disturbance history of the site and the changes in abiotic heterogeneity (e.g., in microtopography and soil moisture), favoring species adapted to disturbances, as well as pioneer and generalist species with strong dispersal and competitive abilities, e.g., *Typha latifolia*, associated with created pools and *Eriophorum vaginatum*, associated with spontaneous pools (Erdős et al., 2018; Holl et al., 2022; Larkin et al., 2016). Comparatively, our results showed that numerous species were more strongly associated with reference pools (20 species), including *Andromeda polifolia, Drosera rotundifolia, Eriophorum virginicum, Gaylussacia baccata, Mylia anomala, Nuphar advena, Rhynchospora alba, Rubus chamaemorus, Sarracenia purpurea, Sphagnum medium, Utricularia cornuta,* and *Vaccinium oxycoccos*. These species, also frequently reported in other studies (Fontaine et al., 2007; Mazerolle et al., 2006), served as indicators for assessing the success of ecological restoration in peatland pools. However, we observed fewer species strongly associated with the three pool types within restored peatlands, likely due to the high variability in species composition within individual pools.

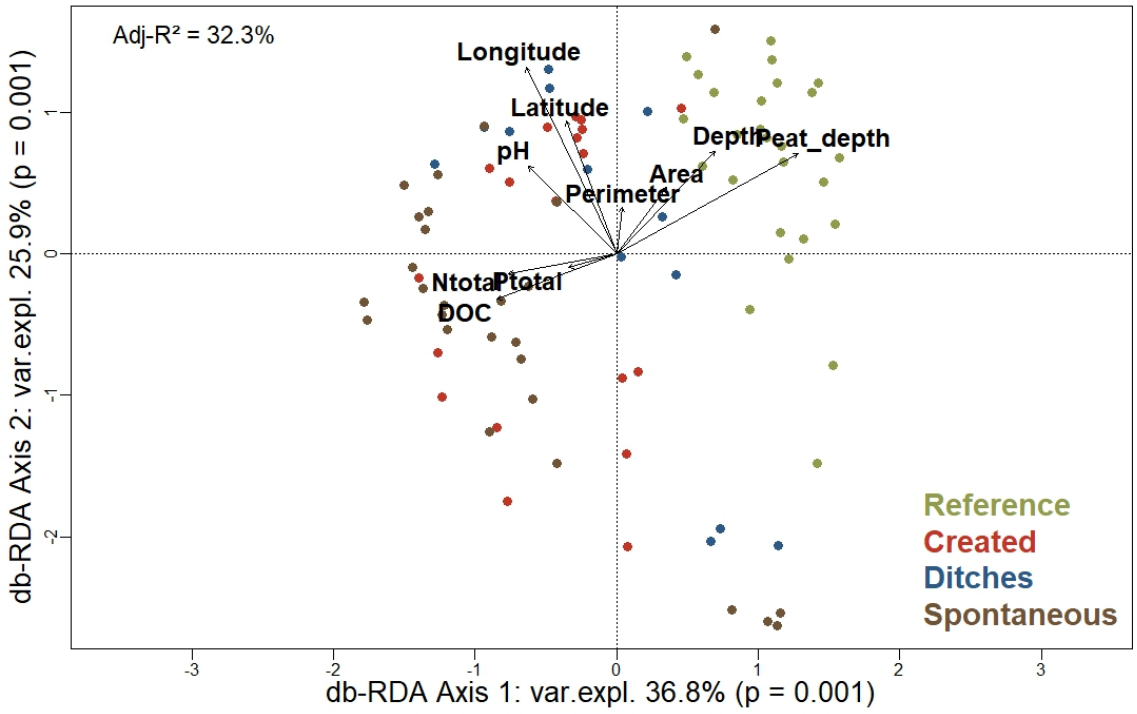

Figure 5.Distance-based redundancy analysis (dbRDA) of the Hellinger distance matrix of plant communities concerning spatial, morphological, and physicochemical variables between the four types of pools in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick) (Adj-R^2 = adjusted-R^2, i.e., proportion of variation in species composition explained by environmental parameters; var.expl = variance explained, i.e., proportion of total variance explained by axes 1 and 2, see Appendix 1.10 for more details).

What are the key environmental variables shaping species diversity and composition?

Species richness, cover, and composition in peatland pools were significantly influenced by environmental variables reflecting both regional gradients and local conditions. Longitude has a positive influence on species cover in typical species associated with bogs, reflecting two climatic gradients: from continental to maritime and from temperate southern Canada (New Brunswick, Lower St. Lawrence, and Quebec) to more boreal northern Quebec (Lac-St-Jean). Northern regions experience colder temperatures and shorter growing seasons, favoring small, fast-growing vascular species and being more resistant to environmental stress (Pinto-Ledezma et al., 2018). In contrast, more southerly areas benefit from warmer climates, potentially supporting a greater composition of species (Pinceloup et al., 2020; Watmough et al., 2022). One example is the presence of *Sphagnum flavicomans*, a species more strongly associated with drainage ditches in our study, which were mainly surveyed in the New Brunswick region (Atlantic Canada). This species is endemic to bogs in the North American Atlantic region because of its tolerance to sea salt spray (Damman, 1995; Davis and Anderson, 2001; Wells, 1996).

Pool depth positively influenced species richness in all the categories: total plant species (TOTAL), species associated with other microforms in bogs (BOG) and pool typical species (POOL). Additionally, greater pool depth increased the cover of species found in other microforms in bogs (BOG). Peacock et al. (2013) demonstrated the relationship between pool depth and associated species, observing that deep pools had a high cover of *Sphagnum* species, a group of species targeted by the ecological restoration of peatlands (Rochefort, 2000). Shallow pools, as is the case of spontaneous pools, on the other hand, showed significantly higher cover of *Eriophorum vaginatum* (Peacock et al., 2013), a species that colonizes bare peat and tolerates drier conditions such as a lower water table (Kivimäki et al., 2008; Lavoie et al., 2005; Poulin et al., 2005). Nevertheless, Lavoie et al. (2003) have shown that colonization by *Eriophorum* does not necessarily lead to restoration failure, as a process of plant succession is initiated that can lead to *Sphagnum* colonization within 5 to 10 years.

The depth of peat around the edges of the pools positively influences plant species richness and cover while shaping their composition. This result is expected because natural pools had greater peat depth than those within restored peatlands, as they are not extracted. However, in restored peatlands, the construction of ditches can expose part of the underlying mineral soil (Armstrong et al., 2009; Quinty and Rochefort, 2003). Indeed, the ditches were located at the bottom of the bed profile, where the peat thickness was generally thinner, resulting in a shallower peat layer that increased contact with the mineral substrate (Armstrong et al., 2009). This altered contact can change nutrient conditions, potentially facilitating the colonization of different vegetation types, including a predominance of vascular species, e.g., ericaceous shrub species (Crowley et al., 2021; González et al., 2014; Räsänen et al., 2023).

Variables related to the chemical properties of pools, such as pH, dissolved organic carbon (DOC) concentration, total phosphorus, and total nitrogen, were generally associated with lower plant richness and cover. DOC, pH, and nitrogen concentration were also key parameters in explaining changes in plant composition. The phenomenon of chemical enrichment was observed in pools within restored peatlands (Jolin et al., 2024). This process contributes to a decline in biodiversity by altering nutrient dynamics, enhancing biomass production through the growth of vascular plants, and restricting the development of other plants, such as mosses. For example, excessively high concentrations of nitrogen and phosphorus may favour the development of vascular plant species, e.g., *Larix* and *Rhododendron* family (Brown and Bates, 1990; Freeman et al., 2004; Larmola et al., 2013; van der Wal et al., 2005). As a keystone species (Rochefort, 2000), *Sphagnum* moss intercepts nitrogen to limit its supply to vascular plants (van der Wal et al., 2005), slowing down decomposition through its recalcitrant litter and acidity (Van Breemen, 1995). However, when nutrient limitation is lifted, vascular plants can gain an advantage due to their greater height, allowing them to outcompete *Sphagnum* mosses for light (Hautier et al., 2009). In the same way, the fluctuations of DOC in peatlands increase the richness of vascular plant species (Chapman et al., 2022; Strack et al., 2008) and reduce the richness and cover of *Sphagnum* moss

by increasing shade, litter production, and evapotranspiration (Limpens et al., 2003; Tomassen et al., 2004). Ecologically restored pools exhibit a higher pH than reference pools (Mazerolle et al., 2006). Our results indicated that a basic pH enhanced overall species richness, while an acidic pH supported species characteristic of bogs. This shift toward a more basic pH thus promotes species that are not the primary targets of restoration efforts (Turner et al., 2016). Finally, pool morphology (perimeter and area) influenced species richness but not species cover, and had a weaker effect on plant composition compared to other environmental variables tested. Since the largest values of perimeter and area were related to reference pools and ditches, our results may have indicated a confounding effect between the values of environmental variables and pool types.

Conclusion

By comparing four types of pools with different environmental conditions, we highlighted significant changes in the diversity and composition of the colonizing plant communities. We observed that changes in pool types were associated with differences in pool water chemistry. Created pools tended to have higher concentrations of nitrogen, phosphorus, and dissolved organic carbon (DOC) than reference pools. This shift favours the colonization and growth of vascular plant species over moss species, such as *Sphagnum* mosses. When possible, pools should therefore be dug as deep as possible, while avoiding exposing the underlying mineral layers. This could allow retaining water throughout the growing season, promote anaerobic conditions, and minimize decomposition and chemical instability. Our results also revealed significant differences in species richness between pool types, particularly for species typical of pools. In terms of cover, the most notable differences were observed between created pools and the other three categories (reference, spontaneous, and ditches). These differences were primarily influenced by the morphology of the pools (depth, perimeter), which acted as ecological filters, restricting plant establishment. We observed that the MLTT restoration technique in *Sphagnum*-dominated peatlands successfully recreated a vegetation cover similar to that of reference pools for typical pool species. However, it did not achieve the same level of species richness observed in the reference pools. Finally, we highlighted that the reference pools exhibited a more homogeneous species pool. In contrast, pools within restored peatlands displayed significant variability in associated species within and between pools. This variability includes preferential colonization by generalist species that are not the primary target of restoration efforts, e.g., *Typha latifolia*. This underscores the necessity of implementing additional restoration methods, such as the reintroduction of pool species, in order to promote the establishment of typical plant biodiversity in peatlands undergoing ecological restoration.

Acknowledgments

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Data availability statement

The data are accessible via the Canadian dataverse repository Borealis, https://doi.org/10.5683/SP3/CPQNP0.

Appendices

Table 1. 1. List of peatlands where pools were sampled, divided between the three types of climatic regions, in ombrotrophic peatlands pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in Eastern Canada (Quebec and New Brunswick). The name of the peatlands and the sector location are provided.

			Type of pool			
Region	**Site and sector**	**Sector location**	**Created**	**Spontanous**	**Ditch**	**Natural**
Atlantica canada	Maisonnette R2000	47.820215,-65.023128	0	0	3	0
	Kent R2008A	46.310623,-65.136837	0	5	3	0
	Pokesudie M2006	47.819770,-64.780825	3	0	0	0
	Inkerman Ferry R2008	47.705859,-64.818340	3	0	0	0
	Baie-Sainte-Anne M2015	46.987330,-64.999917	2	0	0	0
	Miscou	47.9384280,-64.5226109	0	0	0	3
	Black-rock	47.7149709,-65.2725914	0	0	0	3
Great Lakes and St Lawrence	Chemin du Lac R1995	47.768372,-69.526130	0	2	2	0
	Saint-Modeste R2013	47.833743,-69.462967	0	3	0	0
	Président-Ouest R2012	47.786055,-69.491455	0	2	0	0
	Verbois R2006	47.836220,-69.440585	0	6	0	0
	Bois-des-Bel R1995	47.967220,-69.430198	8	0	0	0
	Saint-Fabien-sur-Mer R2011A	48.308628,-68.870688	3	0	0	0
	Saint-Alexandre-du-Kamouraska	47.739855,-69.610953	0	0	0	3

	Saint-Charles-de-Bellechase	46.769227,-71.000235	0	0	0	3
	Grande-Plée-Bleue	46.779833,-71.056853	0	0	0	3
Northeastern Forest	Sainte-Marguerite-Marie AA2001	48.827642,-72.175940	0	5	5	0
	Ascension	48.757045,-71.728222	0	0	0	2
	Saint-Ludger	48.877983,-71.815078	0	0	0	3
	Pointe-Lebel RA2010	49.156588,-68.259053	0	3	0	0
	Escoumins R2011	48.317282,-69.434713	0	1	0	0
	Pointe-Lebel	49.150505,-68.268145	0	0	0	3
	Escoumins	48.3270394,-69.4388613	0	0	0	3

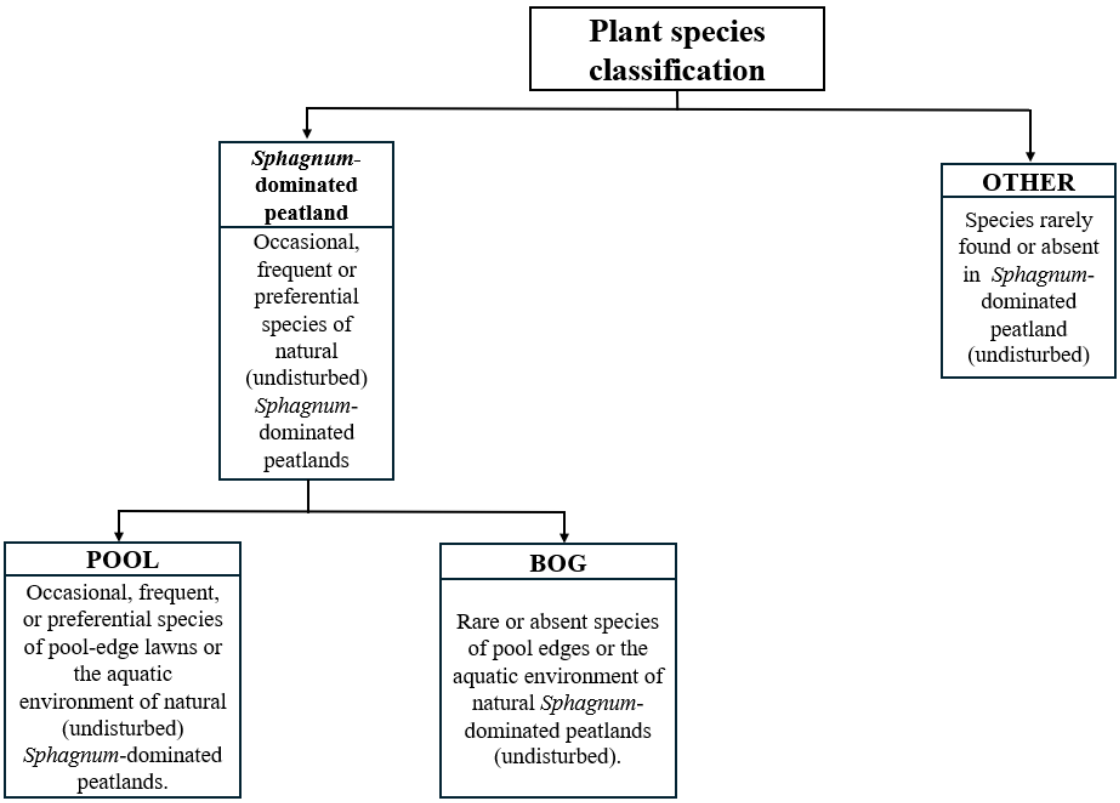

Figure 1. 1. Decision trees were used to categorize each species, and bibliographic sources (Faubert, 2012; Lachance et al., 2021; Lemmer et al., 2023; Morin, 2000; Payette and Rochefort, 2001; Vitt, 2014) were used to classify species according to preferential habitat.

Table 1. 2. List of plant species inventoried in ombrotrophic peatland pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in Eastern Canada (Québec and New Brunswick). For each species, the status of plant functional type (GROUP), scientific name (NAME), species code (ID), frequency, and finally, habitat-specific categories are represented by species typical of other bog microforms (BOG), bog pool species (POOL) and species not typical of peatlands, but of other ecosystems (OTHER), bibliographic sources (Faubert, 2012; Lachance et al., 2021; Lemmer et al., 2023; Morin, 2000; Payette and Rochefort, 2001; Vitt, 2014) were used to classify the habitat-specific category of each specie.

Group	Name	ID	AUTHORS	Freq	Class
Tree	*Betula glandulosa*	bet_gla	Michaux	1.17	OTHER
	Betula papyrifera	bet_pap	Marshall	28.23	OTHER
	Larix laricina	lar_lar	(Du Roi) K. Koch	36.47	BOG
	Picea mariana	pic_mar	(Miller) Britton, Sterns & Poggenburgh	34.11	BOG
	Populus tremuloides	pop_tre	Michaux	1.17	OTHER
	Thuja occidentalis	thu_occ	Linnaeus	3.52	OTHER
Ericaceous shrub	*Kalmia polifolia*	kal_pol	Wangenheim	67.05	BOG
	Rhododendron canadense	rho_can	(Linnaeus) Torrey	25.88	BOG
	Rhododendron groenlandicum	rho_gro	(Oeder) Kron & Judd	80	BOG
	Vaccinium angustifolium	vac_ang	Aiton	40	BOG
	Vaccinium macrocarpon	vac_mac	Aiton	30.58	POOL
	Vaccinium myrtilloides	vac_myr	Michaux	1.17	BOG
	Viburnum cassinoides	vib_cas	Linnaeus	0.07	BOG
Other Shrub	*Alnus incana*	aln_inc	Moench	1.17	OTHER
	Aronia melanocarpa	aro_mel	Elliott	7.05	BOG
	Geocaulon lividum	geo_liv	(Richardson) Fernald	1.17	BOG
	Ilex mucronata	ile_muc	(Linnaeus) M. Powell, V. Savolainen & S. Andrews	0.22	BOG
	Ilex verticillata	ile_ver	(Linnaeus) A. Gray	5.88	OTHER
	Myrica gale	myr_gal	Linnaeus	8.23	BOG
	Salix bebbiana	sal_bib	Sargent	7.05	OTHER

	Salix candida	sal_can	Flüggé ex Willdenow	0.14	OTHER
	Salix pyrifolia	sal_pir	Andersson	1.17	OTHER
	Spiraea alba	spi_alb	Du Roi	10.58	OTHER
	Spiraea alba var. *latifolia*	spi_lat	(Aiton) Dippel	1.17	OTHER
	Spiraea tomentosa	spi_tom	Linnaeus	1.17	OTHER
Graminoid	*Calamagrostis canadensis*	cal_can	Palisot de Beauvois	11.76	OTHER
	Carex canescens	car_can	Linnaeus	38.82	BOG
	Carex limosa	car_lim	Linnaeus	17.64	POOL
	Carex oligosperma	car_oli	Michaux	23.52	BOG
	Carex trisperma	car_tri	Dewey	10.58	BOG
	Carex viridula	car_vir	Michaux	1.17	OTHER
	Eriophorum angustifolium	eri_ang	Honckeny	36.47	BOG
	Eriophorum vaginatum var. *Spissum*	eri_vag	Linnaeus	77.64	BOG
	Eriophorum virginicum	eri_vir	Linnaeus	47.05	BOG
	Juncus balticus	jun_bal	Willdenow	0.29	OTHER
	Juncus effusus	jun_eff	Linnaeus	2.35	OTHER
	Juncus tweedyi	jun_twe	Rydberg	31.76	OTHER
	Muhlenbergia uniflora	muh_uni	(Muhlenberg) Fernald	1.17	OTHER
	Phragmites australis	phr_aus	(Cavanilles) Trinius ex Steudel	1.17	OTHER
	Poa palustris	poa_pal	Linnaeus	1.17	OTHER
	Rhynchospora alba	rhy_alb	(Linnaeus) Vahl	36.47	POOL
	Schoenoplectiella mucronata	sch_muc	(Linnaeus) J. Jung & H.K. Choi	1.17	OTHER
	Schoenoplectus americanus	sch_ame	(Persoon) Volk ex Schinz & R. Keller	1.17	OTHER
	Schoenoplectus pungens	sch_pun	(Vahl) Palla	2.35	OTHER
	Typha latifolia	typ_lat	Linnaeus	23.52	OTHER

	Vaccinium oxycoccos	vac_oxy	Linnaeus	84.70	BOG
Forb	*Alisma triviale*	ali_tri	Pursh	1.17	OTHER
	Alopecurus aequalis	alo_aeq	Sobolewski	2.35	OTHER
	Anaphalis margaritacea	ana_mar	(Linnaeus) Bentham & Hooker f.	0.22	OTHER
	Chamaenerion angustifolium	cha_ang	Scopoli	3.52	OTHER
	Cicuta maculata	cic_mac	Linnaeus	2.35	OTHER
	Claytosmunda claytoniana	cla_cla	(Linnaeus) Metzgar & Rouhan	1.17	OTHER
	Coptis trifolia	cop_tri	(Linnaeus) Salisbury	1.17	OTHER
	Doellingeria umbellata	doe_umb	(Miller) Nees	3.52	OTHER
	Drosera intermedia	dro_int	Hayne	25.88	POOL
	Drosera rotundifolia	dro_rot	Linnaeus	69.41	POOL
	Dryopteris cristata	dry_cri	(Linnaeus) A. Gray	2.35	OTHER
	Dulichium arundinaceum	dul_aru	(Linnaeus) Britton	3.52	OTHER
	Epilobium palustre	epi_pal	Linnaeus	2.35	OTHER
	Equisetum arvense	equ_arv	Linnaeus	1.17	OTHER
	Equisetum fluviatile	equ_flu	Linnaeus	0.07	OTHER
	Equisetum palustre	equ_pal	Linnaeus	1.17	OTHER
	Equisetum pratense	equ_pra	Ehrhart	1.17	OTHER
	Euphrasia nemorosa	eup_nem	(Persoon) Wallroth	1.17	OTHER
	Euthamia graminifolia	eut_gra	(Linnaeus) Nuttall	4.70	OTHER
	Eutrochium maculatum	eut_mac	(Linnaeus) E.E. Lamont	2.35	OTHER
	Fragaria vesca	fra_ves	Linnaeus	1.17	OTHER
	Galium labradoricum	gal_lab	(Wiegand) Wiegand	1.17	OTHER
	Galium palustre	gal_pal	Linnaeus	2.35	OTHER
	Hypericum ellipticum	hyp_ell	Hooker	2.35	OTHER

	Hypericum fraseri	hyp_fra	(Spach) Steudel	14.11	OTHER
	Hypericum mutilum	hyp_mut	Linnaeus	2.35	OTHER
	Hypericum virginicum	hyp_vir	Linnaeus	3.52	OTHER
	Lemna minor	lem_min	Linnaeus	2.35	POOL
	Liparis loeselii	lip_loe	(Linnaeus) Richard	0.14	OTHER
	Lycopus uniflorus	lyc_uni	Michaux	8.23	OTHER
	Lysimachia borealis	lys_bor	(Rafinesque) U. Manns & Anderberg	1.17	OTHER
	Lysimachia thyrsiflora	lys_thy	Linnaeus	2.35	OTHER
	Lythrum salicaria	lyt_sal	Linnaeus	1.17	OTHER
	Maianthemum canadense	mai_can	Desfontaines	1.17	OTHER
	Maianthemum trifolium	mai_tri	(Linnaeus) Sloboda	3.52	BOG
	Melampyrum lineare	mel_lin	Linnaeus	1.17	BOG
	Nuphar advena	nup_adv	(Aiton) W.T. Aiton	27.05	POOL
	Oclemena nemoralis	ocl_nem	(Aiton) Greene	2.35	OTHER
	Onoclea sensibilis	ono_sen	Linnaeus	2.35	OTHER
	Osmundastrum cinnamomeum	osm_cin	(Linnaeus) C. Presl	5.88	OTHER
	Oxalis montana	oxa_mon	Rafinesque	1.17	OTHER
	Pilosella caespitosa	hie_cae	(Dumortier) P.D. Sell & C. West	2.35	OTHER
	Platanthera blephariglottis	pla_ble	(Willdenow) Lindley	0.07	BOG
	Rubus chamaemorus	rub_cha	Linnaeus	18.82	BOG
	Rubus pubescens	rub_pub	Rafinesque	1.17	OTHER
	Sanguisorba canadensis	san_can	Linnaeus	2.35	OTHER
	Sarracenia purpurea	sar_pur	Linnaeus	41.17	BOG
	Scheuchzeria palustris	sch_pal	Linnaeus	8.23	POOL
	Scirpus cyperinus	sci_cyp	(Linnaeus) Kunth	22.35	OTHER

	Solidago rugosa	sol_rug	Miller	5.88	OTHER
	Solidago uliginosa	sol_uli	Nuttall	0.07	BOG
	Sonchus arvensis	son_arv	Linnaeus	2.35	OTHER
	Sparganium emersum	spa_eme	Rehmann	2.35	OTHER
	Sparganium fluctuans	spa_flu	(Morong) B.L. Robinson	1.17	OTHER
	Symphyotrichum novi-belgii	sym_nov	(Linnaeus) G.L. Nesom	0.07	OTHER
	Tussilago farfara	tus_far	Linnaeus	1.17	OTHER
	Utricularia cornuta	utr_cor	Michaux	16.47	POOL
	Utricularia vulgaris	utr_vul	Linnaeus	9.41	POOL
	Viola macloskeyi	vio_mac	F.E. Lloyd	1.17	OTHER
	Impatiens capensis	imp_cap	Meerburgh	1.17	OTHER
Sphagnum moss	*Sphagnum angermanicum*	sph_ange	Melin, Svensk Bot	0	BOG
	Sphagnum angustifolium	sph_ang	(Warnst.) C.E.O. Jensen	44.70	BOG
	Sphagnum capillifolium	sph_cap	(Ehrh.) Hedw	62.35	BOG
	Sphagnum cuspidatum	sph_cus	Ehrh. ex Hoffm.	74.11	POOL
	Sphagnum fallax	sph_fal	H. Klinggr.	74.11	POOL
	Sphagnum fimbriatum	sph_fim	Wils. in Wils. & Hook. f.	4.70	BOG
	Sphagnum flavicomans	sph_fla	(Cardot) Warnst	10.58	BOG
	Sphagnum fuscum	sph_fus	(Schimp.) H. Klinggr	61.17	BOG
	Sphagnum majus	sph_maj	(Russow) C.E.O. Jensen	52.94	POOL
	Sphagnum medium	sph_med	Limpr	81.17	POOL
	Sphagnum papillosum	sph_pap	Lindb	38.82	POOL
	Sphagnum riparium	sph_rip	Ångström	5.88	POOL
	Sphagnum rubellum	sph_rub	Wilson	87.05	BOG
	Sphagnum russowii	sph_rus	Warnst	7.05	BOG
	Sphagnum squarrosum	sph_squ	Crome	2.35	OTHER
	Sphagnum torreyanum	sph_tor	Sullivant	0	POOL

	Sphagnum warnstorfii	sph_war	Russow	1.17	OTHER
Moss	*Straminergon stramineum*	str_str	(Dicks. ex Brid.) Hedenäs	1.17	OTHER
	Warnstorfia fluitans	wan_flu	(Hedw.) Loeske	45.88	POOL
	Aulacomnium palustre	aul_pal	(Hedw.) Schwägr	11.76	BOG
	Dicranum groenlandicum	dic_gro	Brid	0.07	OTHER
	Dicranum leioneuron	dic_lei	Kindb	2.35	BOG
	Dicranum montanum	dic_mon	Hedw	0.07	OTHER
	Dicranum polysetum	dic_pol	Swartz	20	BOG
	Dicranum undulatum	dic_und	Schrad. ex Brid	31.76	BOG
	Fontinalis hypnoides	fon_hyp	Hartm	1.17	POOL
	Pohlia nutans	poh_nut	(Hedw.) Lindb.	11.76	BOG
	Polytrichum commune	pol_com	Hedw	2.35	BOG
	Polytrichum strictum	pol_str	Menzies ex Brid	72.94	BOG
	Ptilium crista-castrensis	pti_cri	(Hedw.) De Not	3.52	OTHER
	Scorpidium cossonii	sco_cos	(Schimp.) Hedenäs	1.17	OTHER
	Gymnocolea inflata	gym_inf	(Huds.) Dumort.	38.82	POOL
Liverwot	*Mylia anomala*	myl_ano	(Hook.) Gray	70.58	BOG
	Odontoschisma fluitans	odo_flu	(Nees) Jørg	3.52	POOL
	Pellia epiphylla	pel_epi	(L.) Corda	4.70	OTHER
	Ptilidium ciliare	pti_cil	(L.) Hampe	16.47	BOG

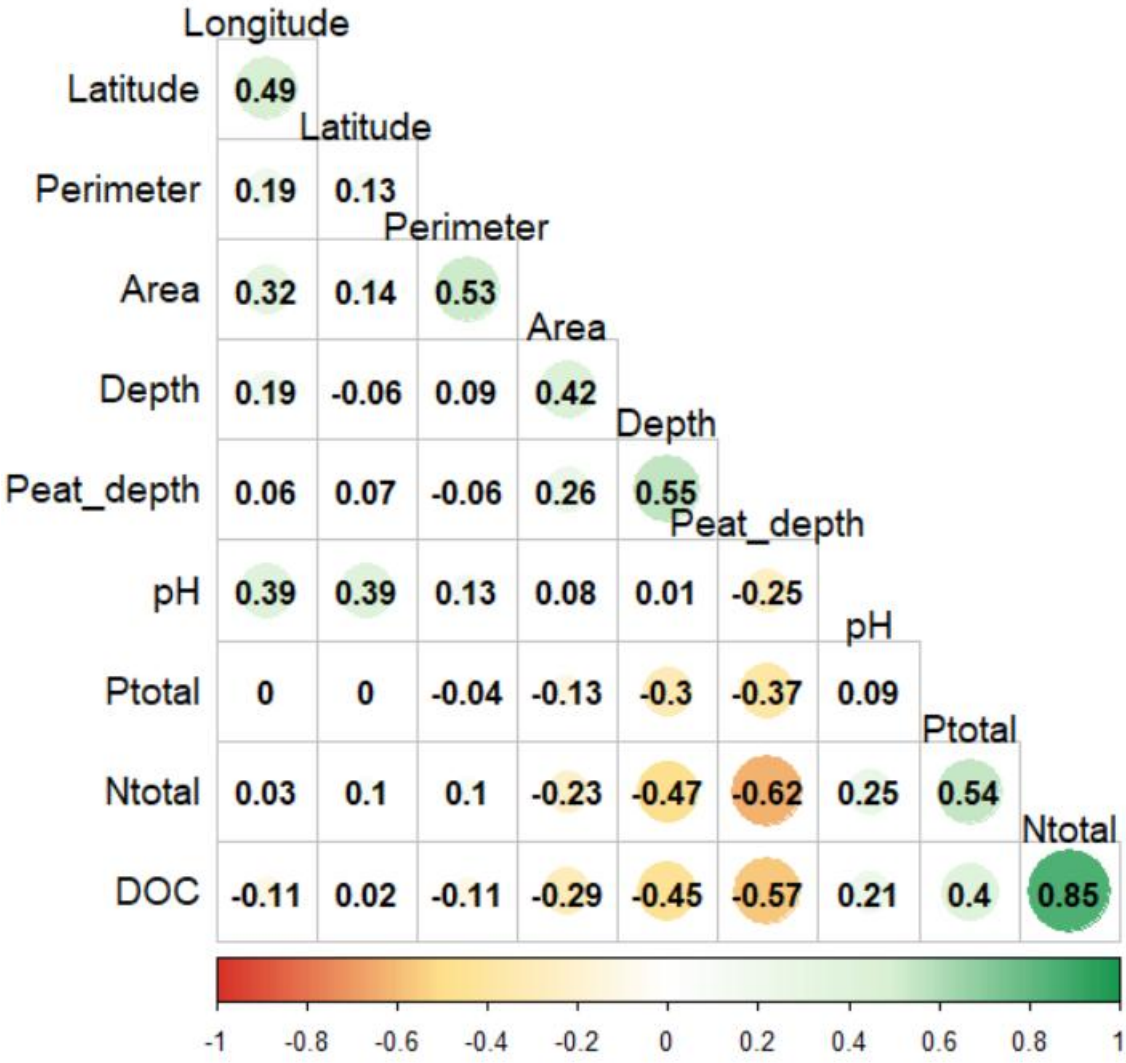

Figure 1. 2. Correlation matrix of the environmental conditions: Longitude, Latitude, Perimeter, Area, Pool depth, Peat depth, pH, total phosphorus (P_{total}), total nitrogen (N_{total}) and dissolved organic carbon (DOC), used to model variations in habitat-specific species richness and total cover for the four types of pools in the ombrotrophic peatlands (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in Eastern Canada (Quebec and New Brunswick). Values refer to r = Pearson product-moment correlation coefficient, CI = confidence interval.

Table 1. 3. Spatial, morphological, and chemical conditions, comparisons between the different types of pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick).

			Reference pools			Restored pools		
Variable	**F-value**	**p-value**	**Reference vs Created**	**Reference vs Ditches**	**Reference vs Spontaneous**	**Created vs Ditches**	**Created vs Spontaneous**	**Ditches vs Spontaneous**
Longitude	0.119	0.949						
Latitude	1.953	0.128						
Perimeter	56.738	**<0.0001**	0.118	**<0.0001**	0.054	**<0.0001**	1.000	**<0.0001**
Area	4.687	**0.005**	**0.026**	0.651	**0.006**	0.555	0.997	0.390
Depth	15.884	**<0.0001**	**0.002**	**0.001**	**<0.0001**	0.907	0.069	0.449
Peat_depth	69.435	**<0.0001**	**0.000**	**<0.0001**	**<0.0001**	0.187	**0.006**	0.826
pH	2.081	0.109						
P_{total}	4.661	**0.005**	0.760	0.139	**0.004**	0.610	0.119	0.903
N_{total}	29.230	**<0.0001**	**0.020**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.918
DOC	18.733	**<0.0001**	**0.000**	**<0.0001**	**<0.0001**	0.791	0.075	0.635

Table 1. 4. Estimate coefficients ((± SE)) and confidence intervals (95% CI) for each environmental variable used to predict variations in plant species cover and richness between the four types of pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]) in the ombrotrophic peatlands, in Eastern Canada (Quebec and New Brunswick). Habitat-specific categories are represented by the total species (TOTAL), species typical of other bog microforms (BOG), and bog pool species (POOL).

Variable	Total Cover		Cover Pool		Cover Bog	
	Estimate ± SE	95% CI	Estimate ± SE	95% CI	Estimate ± SE	95% CI
Longitude (°)	0.104 ± 0.143	-0.177; 0.385	-0.014 ± 0.246	-0.496; 0.468	0.496 ± 0.212	0.081; 0.911
Latitude (°)	0.182 ± 0.133	-0.078; 0.441	0.164 ± 0.231	-0.289; 0.618	0.457 ± 0.203	0.058; 0.855
Perimeter (m)	0.001 ± 0.060	-0.117; 0.118	0.000 ± 0.092	-0.179; 0.180	0.095 ± 0.081	-0.064; 0.253
Area (m^2)	0.016 ± 0.062	-0.106; 0.138	0.053 ± 0.096	-0.134; 0.241	0.036 ± 0.085	-0.131; 0.204
Pool Depth (cm)	0.004 ± 0.073	-0.139; 0.146	-0.051 ± 0.113	-0.272; 0.169	0.209 ± 0.100	0.014; 0.404
Peat depth (cm)	0.221 ± 0.101	0.022; 0.419	0.157 ± 0.173	-0.182; 0.496	0.437 ± 0.149	0.146; 0.729
pH	-0.168 ± 0.070	-0.304; -0.031	-0.246 ± 0.109	-0.459; -0.032	-0.143 ± 0.098	-0.335; 0.049
P_{total} (mg/L)	-0.090 ± 0.067	-0.221; 0.041	-0.056 ± 0.104	-0.260; 0.148	-0.179 ± 0.092	-0.359; 0.000
N_{total} (mg/L)	-0.143 ± 0.085	-0.310; 0.025	-0.244 ± 0.137	-0.512; 0.024	-0.026 ± 0.127	-0.275; 0.224
DOC (mg/L)	-0.251 ± 0.082	-0.412; -0.090	-0.270 ± 0.138	-0.541; 0.000	-0.171 ± 0.129	-0.423; 0.081
Variable	Total Richness		Richness Pool		Richness Bog	
	Estimate ± SE	95% CI	Estimate ± SE	95% CI	Estimate ± SE	95% CI
Longitude (°)	0.026 ± 0.054	-0.079; 0.132	0.021 ± 0.080	-0.136; 0.177	0.032 ± 0.058	-0.081; 0.145
Latitude (°)	0.063 ± 0.050	-0.036; 0.161	0.074 ± 0.076	-0.076; 0.223	0.051 ± 0.055	-0.057; 0.160
Perimeter (m)	0.078 ± 0.030	0.020; 0.136	0.029 ± 0.051	-0.072; 0.129	0.101 ± 0.036	0.031; 0.171

Area (m^2)	0.066 ± 0.029	0.008; 0.124	0.048 ± 0.052	-0.054; 0.149	0.072 ± 0.036	0.001; 0.142
Depth (cm)	0.084 ± 0.032	0.021; 0.146	0.143 ± 0.054	0.038; 0.248	0.108 ± 0.038	0.033; 0.182
Peat depth (cm)	0.098 ± 0.038	0.024; 0.173	0.266 ± 0.046	0.177; 0.356	0.120 ± 0.043	0.036; 0.204
pH	0.066 ± 0.033	0.002; 0.130	-0.037 ± 0.060	-0.156; 0.081	0.014 ± 0.040	-0.065; 0.092
P_{total} (mg/L)	-0.013 ± 0.031	-0.075; 0.049	-0.160 ± 0.055	-0.268; -0.053	-0.043 ± 0.037	-0.116; 0.030
N_{total} (mg/L)	-0.028 ± 0.038	-0.102; 0.045	-0.202 ± 0.049	-0.298; -0.106	-0.030 ± 0.043	-0.115; 0.055
DOC (mg/L)	-0.013 ± 0.038	-0.088; 0.062	-0.210 ± 0.055	-0.318; -0.103	-0.031 ± 0.044	-0.117; 0.055

Table 1. 5. Habitat-specific species richness and total cover, comparisons between the different types of pools (reference pools [n = 26], created pools [n = 19], drainage ditches [n = 13], spontaneous pools [n = 27]) in ombrotrophic peatlands in Eastern Canada (Quebec and New Brunswick). Habitat-specific categories are represented by the cover and richness of total species (TOTAL), species typical of other bog microforms (BOG), and bog pool species (POOL).

				Reference pools			Restored pools		
	Variable	**F-value**	**p-value**	**Reference vs Created**	**Reference vs Ditches**	**Reference vs Spontaneous**	**Created vs Ditches**	**Created vs Spontaneous**	**Ditches vs Spontaneous**
Richness	TOTAL	8.37	**<0.0001**	0.8851	0.2383	**<0.0001**	0.6430	**0.0030**	0.2206
	POOL	31.88	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9123	0.1014	0.5290
	BOG	8.49	**<0.0001**	0.5742	0.9995	**<0.0001**	0.7620	**0.0218**	**0.0025**
Cover	TOTAL	9.84	**<0.0001**	**<0.0001**	0.6513	0.2449	**0.0060**	**0.0024**	0.9840
	POOL	2.61	0.057						
	BOG	16.25	**<0.0001**	**<0.0001**	0.1291	**<0.0001**	**0.0074**	0.3303	0.1880

Table 1. 6. Results for the PERMANOVA analysis between the four types of pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in the *Sphagnum*-dominated peatlands, in Eastern Canada (Quebec and New Brunswick). The **p value** is the p-value for each pairwise comparison, and finally, **p adjusted** is the adjusted p-value, which corrects for multiple comparisons.

Pairs	df	Sum of squares (SS)	F model	R^2	p value	p adjusted
Ditches vs Created	1	1.9	3.6	0.10	0.001	**0.001**
Ditches vs Reference	1	2.9	7.8	0.17	0.001	**0.001**
Ditches vs Spontaneous	1	1.6	2.7	0.06	0.003	**0.003**
Created vs Reference	1	4	9.9	0.19	0.001	**0.001**
Created vs Spontaneous	1	1.3	2.1	0.04	0.021	0.021
Reference vs Spontaneous	1	6.6	13.8	0.21	0.001	**0.001**

Table 1. 7. Results for the PERMDISP analysis between the pools, in the *Sphagnum*-dominated peatlands, in Eastern Canada (Quebec and New Brunswick). The **Pr(>F)** is the p-value associated with the F-test.

	Df	Sum of squares	Mean of squares	F value	Pr (>F)
Groups	3	0.87	0.29	13.5	**3.093e-07**
Residual	81	1.73	0.02		

Table 1. 8. List of plant species significantly associated with the four types of pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in the ombrotrophic peatlands, in Eastern Canada (Quebec and New Brunswick) (based on the phi coefficient of association).

Type of pool	Name sp.	phi	p-value
Reference	*Rhynchospora alba*	0.738	0.001
	Sphagnum fuscum	0.679	0.001
	Drosera rotundifolia	0.653	0.001
	Kalmia polifolia	0.608	0.001
	Sarracenia purpurea	0.591	0.001
	Andromeda polifolia	0.575	0.001
	Kalmia angustifolia	0.550	0.001
	Rubus chamaemorus	0.523	0.001
	Nuphar advena	0.492	0.001
	Picea mariana	0.491	0.001
	Mylia anomala	0.483	0.002
	Sphagnum medium	0.478	0.002
	Sphagnum rubellum	0.472	0.001
	Eriophorum virginicum	0.457	0.001
	Gaylussacia baccata	0.449	0.001
	Gymnocolea inflata	0.447	0.001
	Dicranum undulatum	0.405	0.002
	Utricularia cornuta	0.328	0.009
	Empetrum nigrum	0.325	0.014
	Vaccinium oxycoccos	0.262	0.037
Created	*Hypericum fraseri*	0.441	0.001
	Vaccinium macrocarpon	0.428	0.002
	Typha latifolia	0.362	0.006
	Doellingeria umbellata	0.312	0.029
	Lycopus uniflorus	0.308	0.025
Ditches	*Vaccinium angustifolium*	0.456	0.001
	Rhododendron groenlandicum	0.442	0.001
	Sphagnum russowii	0.385	0.003
	Sphagnum majus	0.316	0.019
	Larix laricina	0.293	0.035
	Sphagnum flavicomans	0.284	0.042
Spontaneous	*Eriophorum vaginatum*	0.395	0.004
	Sphagnum fallax	0.353	0.005
	Scirpus cyperinus	0.264	0.048

Table 1. 9. All *a priori* models predicting variations in plant species cover and richness between the four types of pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]), in the ombrotrophic peatlands, in Eastern Canada (Quebec and New Brunswick), as assessed with Akaike's information criterion corrected for small sample size (AICc). The number of parameters estimated (k), AICc, delta AICc (ΔAICc), AICc weight (W) and adjusted coefficient of determination for fixed only (R^2) are provided.

Measure	Variable	Candidate model	k	AICc	ΔAICc	W	R2
Cover	TOTAL	DOC	4	143.1	0.000	0.537	0.136
		pH	4	145.3	2.127	0.185	0.057
		Peat_depth	4	146.3	3.204	0.108	0.094
		Ntotal	4	148.4	5.272	0.038	0.042
		Null	3	148.8	5.637	0.032	0.000
		Latitude	4	149.1	5.986	0.027	0.063
		Ptotal	4	149.2	6.080	0.026	0.016
		Longitude	4	150.4	7.307	0.014	0.021
		Area	4	150.9	7.770	0.011	0.001
		Depth	4	151.0	7.838	0.011	0.000
		Perimeter	4	151.0	7.840	0.011	0.000
	POOL	pH	4	222.1	0.000	0.330	0.047
		DOC	4	223.2	1.189	0.182	0.055
		Ntotal	4	223.7	1.612	0.148	0.043
		Null	3	224.6	2.584	0.091	0.000
		Peat_depth	4	226.0	3.958	0.046	0.017
		Latitude	4	226.3	4.274	0.039	0.019
		Area	4	226.5	4.467	0.035	0.002
		Ptotal	4	226.6	4.498	0.035	0.002
		Depth	4	226.6	4.578	0.033	0.002
		Longitude	4	226.8	4.784	0.030	0.000
		Perimeter	4	226.8	4.788	0.030	0.000
	BOG	Peat_depth	4	201.9	0.000	0.511	0.158
		Longitude	4	204.8	2.872	0.122	0.187
		Latitude	4	205.2	3.237	0.101	0.161
		Depth	4	205.6	3.699	0.080	0.038
		Ptotal	4	206.1	4.133	0.065	0.027
		Null	3	207.7	5.711	0.029	0.000
		pH	4	207.7	5.737	0.029	0.016
		DOC	4	208.2	6.271	0.022	0.024
		Perimeter	4	208.5	6.519	0.020	0.007
		Area	4	209.7	7.731	0.011	0.001

		Ntotal	4	209.8	7.876	0.010	0.001
Richness	TOTAL	Perimeter	3	556.8	0.000	0.319	0.063
		Depth	3	557.4	0.571	0.240	0.090
		Peat_depth	3	558.0	1.233	0.172	0.122
		Area	3	558.8	2.004	0.117	0.048
		pH	3	559.8	3.034	0.070	0.050
		Null	2	561.9	5.085	0.025	0.000
		Latitude	3	562.5	5.689	0.019	0.047
		Ntotal	3	563.5	6.663	0.011	0.010
		Longitude	3	563.8	6.994	0.010	0.008
		Ptotal	3	563.9	7.056	0.009	0.002
		DOC	3	563.9	7.117	0.009	0.002
	POOL	Peat_depth	3	365.7	0.000	0.997	0.324
		DOC	3	378.9	13.186	0.001	0.207
		Ntotal	3	379.1	13.424	0.001	0.203
		Ptotal	3	383.6	17.975	0.000	0.132
		Depth	3	384.7	19.027	0.000	0.100
		Null	2	389.0	23.298	0.000	0.000
		Latitude	3	390.2	24.500	0.000	0.024
		Area	3	390.3	24.603	0.000	0.010
		pH	3	390.7	25.065	0.000	0.006
		Perimeter	3	390.8	25.131	0.000	0.004
		Longitude	3	391.0	25.379	0.000	0.002
	BOG	Perimeter	3	497.9	0.000	0.366	0.082
		Depth	3	498.3	0.377	0.303	0.104
		Peat_depth	3	498.9	0.996	0.222	0.129
		Area	3	502.1	4.178	0.045	0.044
		Null	2	504.1	6.180	0.017	0.000
		Ptotal	3	504.9	6.991	0.011	0.017
		Latitude	3	505.4	7.450	0.009	0.024
		DOC	3	505.7	7.824	0.007	0.009
		Ntotal	3	505.7	7.842	0.007	0.008
		Longitude	3	505.9	8.013	0.007	0.009
		pH	3	506.1	8.213	0.006	0.002

Table 1. 10. Results for the db-RDA analysis for each environmental variable used to predict plant composition between the four types of pools (reference [n = 26], created [n = 19], ditches [n = 13], spontaneous [n = 27]) in the ombrotrophic peatlands, in Eastern Canada (Quebec and New Brunswick).

Variables	Codes	Df	Variance	F	Pr(>F)	% Intrinsic	% Total (constrained)
	Long	1	3.6577	9.079	0.001	**24.0**	18.1
	Peat depth	1	3.3808	8.3916	0.001	**22.2**	16.7
	pH	1	1.3017	3.231	0.002	**8.5**	6.4
	DOC	1	1.2339	3.0628	0.003	**8.1**	6.1
	Latitude	1	1.1301	2.8051	0.002	**7.4**	5.6
	N_{total}	1	1.1301	2.8052	0.003	**7.4**	5.6
	Perimeter	1	1.0801	2.6809	0.005	**7.1**	5.4
	Area	1	0.9991	2.48	0.01	**6.6**	4.9
	Depth	1	0.7884	1.9569	0.035	**5.2**	3.9
	P_{total}	1	0.5509	1.3674	0.162	**3.6**	2.7
	Residual	74	29.8131				
	Constrained	10	15.2528			**100.0**	

Chapitre 2 Where the Water Settles: Exploring the Ecological Drivers of Plant Communities in Restored Minerotrophic Peatland Pools

2.1 Résumé

Les mares des tourbières abritent une biodiversité distincte, mais l'extraction de la tourbe entraîne souvent leur disparition. Cette étude compare des mares restaurées (créées et spontanées) (n = 21) et de référence (naturelles) (n = 15) au Manitoba et au Québec. La composition végétale diffère fortement entre les mares du Manitoba (Forêt nord-ouest) et les mares du Québec (Basses-terres du Saint-Laurent), avec des contrastes plus marqués dans les mares de référence que dans les restaurées. Le type de mare influence cette composition. Les mares spontanées sont les plus hétérogènes et se divisent selon les régions climatiques. Dans les Basses-terres, elles sont dominées par des espèces comme *Typha latifolia*, associées à une diversité réduite. Les mares créées présentent une richesse plus élevée, mais incluent des espèces non typiques comme *Sonchus arvensis*. Ces résultats montrent que le contexte régional et le type de mare jouent un rôle clé dans la structuration des communautés végétales, et soulignent la nécessité d'adapter les stratégies de restauration aux conditions environnementales locales.

2.2 Abstract

Peatland pools are water-filled habitats that host biodiversity distinctive from the main peatland expanse, serving as refuges for several plant species found exclusively in these environments. However, resource extraction severely degrades these ecosystems through the removal of vegetation and drainage, often resulting in the complete loss of pools. This study, done in different regional contexts of horticultural peat extraction, compared vegetation composition and environmental conditions in 21 pools from six restored moderately rich fens (≥ 6 years post-restoration) and 15 pools from two natural reference peatlands, located in the Northwestern Forest (Manitoba) and St. Lawrence Lowlands (Quebec). We examined two types of restored pools: those actively created and those that formed spontaneously. Vegetation composition differed significantly between pools in the Northwestern Forest and St. Lawrence Lowlands climatic regions, with differences being markedly stronger among the regional reference pools than among the restored pools. Pool type also influenced vegetation composition, with notable differences between reference sites and those under restoration. Spontaneous pools exhibited the greatest inter-pool heterogeneity, separating into two ecological groups categorized by the type of plant species associated with the two distinctive climatic regions. In St. Lawrence lowlands (sub-maritime climate), spontaneous pools were dominated by wetland species, particularly taxa such as Typha latifolia, which

was correlated with a reduced overall pool diversity. Created pools supported greater pool species richness than spontaneous pools but included numerous non-wetland species (e.g., Sonchus arvensis). In the Northeastern Forest (continental climate), species composition remained relatively homogeneous, even in restored pools. Variation in species composition among pools was primarily explained by location, water calcium concentration and electrical conductivity, which together accounted for 38.7% of the total variation. These findings underscore the importance of both regional context and pool creation in shaping plant communities, highlighting the need for restoration strategies that are adapted to regional environmental conditions.

Keywords: open water bodies, aquatic plant species, peatland pools, minerotrophic peatlands, Quebec, Manitoba, abiotic parameters, water chemistry.

Introduction

Canada hosts the world's second-largest peatland area (119 million hectares; Rochefort et al., 2022), with minerotrophic peatlands (fens) representing about 32% of this total (Tarnocai et al., 2000). Regardless of fen subtypes (e.g., basin fens, string fens) (Rydin and Jeglum, 2013), fens display a complex microtopography that includes various microforms such as hummocks, depressions, flarks, pools, and, in specific subtypes like string fens, elongated ridges called strings (Payette and Rochefort, 2001; Vitt et al., 2022). Pools provide habitat for specialized flora and fauna in peatlands (Beadle et al., 2015) and facilitate the colonization of bryophyte species such as *Scorpidium* spp., several liverworts, water-preferring *Sphagnum* species, sedges, and various aquatic and carnivorous plants. Due to this rich and specialized biodiversity, pools can be considered "small natural features (SNFs)" (Hunter et al., 2017), whose ecological importance is disproportionately large relative to their limited spatial extent in the landscape (Groves and Game, 2016; Hunter et al., 2017; Poschlod and Braun-Reichert, 2017). Although pools are characteristic features of peatland ecosystems, the factors that determine their biodiversity remain poorly understood.

Minerotrophic peatland pools occur mainly in boreal and subarctic regions (Warner, 2005; Warner and Asada, 2006), typically in glacial plains and lowlands where hydrology is strongly influenced by the groundwater table (Devito et al., 2017; Vitt et al., 2022). In these cold regions, short growing seasons and low temperatures reduce peat decomposition, favouring net accumulation and the development of a distinct microtopography (Foster, 1989; Glaser and Janssens, 1986). Furthermore, in humid regions, precipitation exceeds evapotranspiration, ensuring the long-term water supply and pool persistence (Holden, 2006). In minerotrophic systems, groundwater and precipitation inputs create flooded depressions (flarks, pools) separated by peat ridges. As a result, patterned fens with pools (string or ribbed fens) are concentrated in central and northern Canada, particularly in Manitoba, Ontario, and northern Quebec, whereas southern fens are more uniform and less strongly patterned (Vitt et al., 2024). These regional and hydrological drivers not only determine where pools

occur across the landscape (Belyea, 2007; Arlen-Pouliot and Payette, 2015) but also strongly influence their ecological characteristics, including the vegetation and water chemistry that develop within pools and along their margins (Turner et al., 2016; Vanschoenwinkel et al., 2009).

Pools in undisturbed fens (hereafter reference pools) exhibit distinctive vegetation and water chemistry. They are typically occupied by aquatic plant communities, often including carnivorous species, while their margins consist of gently sloping flats dominated by brown mosses and sedges (Chee and Vitt, 1989; Vitt et al., 2022). The unique vegetation associated with fen pools is partly related to their hydrochemical conditions. Compared with the surrounding peatland, pool waters often contain higher concentrations of dissolved minerals, particularly calcium, and may exhibit higher pH values (Schwintzer, 1978; Slack et al., 1980; Andersen et al., 2011). These conditions favor the establishment of calciphilous brown mosses and other plant species characteristic of minerotrophic peatlands. For example, pools in a rich fen in the Hudson Bay Lowlands were described as dominated by *Utricularia vulgaris*, *U. intermedia*, *U. minor*, various *Carex* and *Juncus* species, and brown mosses such as *Scorpidium* and *Campylium* species (Sjörs, 1959). Similarly, moderately rich fen pools in western Alberta were dominated by species such as *Scorpidium scorpioides*, *S. revolvens*, and *Carex limosa* (Slack et al., 1980; Vitt & House, 2021).

In Canada, peatlands are affected by various disturbances, including drainage for agricultural purposes, forestry, and flooding resulting from hydroelectric development. Although peat extraction covers a smaller area, it still generates substantial ecological impacts, particularly in sites used for horticultural extraction areas (Pellerin and Poulin, 2013; Rochefort et al., 2022). Peat extraction involves several stages, including 1) the construction of drainage ditches that lower the water table and 2) the removal of surface vegetation (Price et al., 2003; Rochefort et al., 2016). Following peat extraction, typical peatland species often require several decades to recolonize the site, and some characteristic species may never return (Allan et al., 2024; Poulin et al., 2005). Modified abiotic conditions can lead to the emergence of vegetation uncharacteristic of natural peatlands (Graf et al., 2008; Pasquet et al., 2015). As a result, post-extraction sites often differ markedly from their pre-disturbance state, both in species composition and in ecosystem function, making ecological restoration essential to recover peatland biodiversity (Bérubé et al., 2017; Campeau et al., 2004; Chimner et al., 2017).

Ecological restoration in peatlands aims to re-establish functional ecosystems capable of supporting rich biodiversity and providing essential ecosystem services, and in fens, these efforts include approaches designed to promote the recovery of key ecosystem functions, such as carbon capture, and the re-establishment of fen-typical vegetation (Alexandrov et al., 2020; González et al., 2014; Lamers et al., 2015; Nugent et al., 2018). The restoration approaches include adaptations of the moss layer transfer technique (Rochefort et al., 2016; Khan et al., 2025), which have shown promising outcomes for the recovery of vascular plant communities, though

results for bryophyte establishment remain variable in the North American context. Other studies on active rewetting have reported that distinct plant communities can regenerate naturally without the need for vegetation reintroduction (Schwieger et al., 2021; Timmermann et al., 2006; Turmel-Courchesne et al., 2023). However, rewetted fen peatlands in Europe often differ from near-natural fens in terms of biodiversity and ecosystem functioning, particularly in terms of plant community composition and geochemistry (Kreyling et al., 2021). These differences likely reflect contrasting historical contexts: in Europe, most fens have been converted for agricultural use and have consequently disappeared or become severely degraded (Klimkowska et al., 2010), whereas in North America, efforts towards fen restoration are mostly done by the horticultural peat industry (Rochefort et al., 2022). While each method has yielded valuable insights, there is no clear consensus on the most effective approach, partly due to limited reproducibility across sites and the scarcity of long-term studies. This highlights the importance of evaluating restoration outcomes across diverse ecological contexts and extended timescales (Bourgeois et al., 2018; Khan et al., 2025).

The North American guide to peatland restoration (Quinty and Rochefort, 2003) recommends the creation of pools following peat extraction to enhance wildlife habitat and overall biodiversity (Mazerolle et al., 2005). The guide, created for ombrotrophic pools, recommends creating pools between 75 and 150 m² in area and 1–2 m deep, with asymmetrical slopes, one side steep and the other gentle, to mimic natural pool morphology and ensure water retention throughout the growing season. However, despite efforts to replicate natural pool morphology, the use of machinery often results in more angular shapes with predominantly steep edges, and water presence mostly depends on rewetting success rather than pool size and depth (Beadle et al., 2015; Jolin et al., 2024). Furthermore, restoration operations have been deployed to reintroduce plant species such as sedges and bryophytes along the edges of created pools in fens; these efforts have generally helped to establish satisfactory fen vegetation cover (Bourgeois et al., 2018; Drapeau Picard et al., 2021). Besides these active actions, water can naturally accumulate in low-lying areas or man-made depressions during restoration works, where vegetation gradually establishes around the edges, leading to the formation of spontaneous pools (L. Rochefort, personal observations).

This study aimed to deepen our understanding of the vegetation development around three types of pools in fens: natural pools (serving as reference ecosystems), created pools actively designed during peatland restoration, and spontaneous pools that formed passively in low-lying areas during restoration activities, across two climatic regions: the Northeastern Forest and St. Lawrence lowland. We examined how both local environmental conditions and broader regional factors influence vegetation establishment between 6 and 35 years after restoration. We pursued three main objectives: (1) to compare plant species composition patterns among the three pool types (reference, created, and spontaneous) across the two regions (Northeastern Forest

and St. Lawrence Lowlands), and (2) to identify the environmental variables driving plant species composition toward fen pool communities.

Materials and Methods

Study sites

The study was conducted in two provinces, Manitoba and Quebec, focusing on two specific regions: the Eastman region in Manitoba and the Bas-Saint-Laurent region in Quebec (Figure 6). These two provinces correspond to two climatic regions (Environment and Climate Change Canada, 2023): Northwestern Forest (Manitoba) and Great Lakes/St Lawrence Lowlands (Quebec) (Figure 6). Peatlands in the Northwestern Forest were located near St-Labre, which experiences a cold continental climate, a mean annual air temperature of 2°C, a total yearly precipitation of 1200 mm, and a growing season lasting 120 days (Climate normals for St. Labre station, Environment and Climate Change Canada, 2023). Peatlands located in the St Lawrence Lowland region were located near Rivière-du-Loup, which has a warmer sub-maritime climate with warm summers and cold winters, a mean annual air temperature of 3.2°C, total annual precipitation of 1.000 mm, and a growing season of 150 days (Climate normal for Rivière-du-Loup station, Environment and Climate Change Canada, 2023).

A total of 36 pools were sampled in two peatland types (reference and restored) across the two climatic regions: 15 pools distributed in two reference peatlands (one peatland in the Northwestern Forest (Manitoba) and one in St Lawrence lowland (Quebec), and 21 pools sampled in six restored peatlands, three in the Northwestern Forest and three in St Lawrence lowland (Figure 6 and Table 2.1). The reference peatland in the Northwestern Forest (St-Labre region) was classified as an extremely rich fen, characterized by an average pool water pH of 7.2 and electrical conductivity of 266 µS/cm (Turmel-Courchesne, 2019; Vitt, 2006). This reference peatland corresponds to a string fen (Northern Ribbed Fen) under the Canadian Wetland Classification System (National Wetlands Working Group, 1997), i.e., characterized by parallel peat ridges and wet depressions (flarks) oriented perpendicular to groundwater flow, creating elongated pools. This microtopographic gradient shaped the vegetation, with fen brown mosses (e.g., *Scorpidium cossonii*, *Tomentypnum nitens*, *Aulacomnium palustre*) and graminoids (e.g., *Carex aquatilis*) typically occupying the flark margins, whereas peat ridges are dominated by shrubs (e.g., *Myrica gale*, *Salix* spp.) and small trees (e.g., *Larix laricina*) (Vitt et al., 2022). In contrast, the reference peatland in St Lawrence lowland (Lac Caouette) was classified as a moderately rich fen, exhibiting an average pool water pH of 7.0 and electrical conductivity of 178 µS/cm (Bérubé et al., 2017). This peatland corresponds to a riparian (shore) fen that develops along lake margins, where peat accumulates into a stable, non-floating mat. Its relatively flat surface supports communities arranged along subtle microtopographic gradients, dominated by fen brown mosses (e.g., *Campylium stellatum*, *Scorpidium scorpioides*), graminoids (e.g., *Carex* spp.), and aquatic species such as *Utricularia* spp. (Drapeau Picard et al., 2021).

The restored peatlands were also classified as minerotrophic, based on the chemistry of pool waters. In our pools, water exhibited pH values ranging from 4.8–7.4 and electrical conductivity between 37–402 µS/cm, which are consistent with minerotrophic conditions. For context, Andersen et al. (2011) reported peat pH values of 5.7–7.3 and electrical conductivity of 111–470 µS/cm for minerotrophic fens. Although these reference values are based on surrounding peat rather than pool water, both datasets indicate conditions typical of fen ecosystems. Restoration approaches were applied after the cessation of peat extraction activities for horticultural purposes, but varied across peatlands due to the lack of a standardized technique for fens (Table 2.1). In the Northwestern Forest, both the interval between peat extraction and the initiation of restoration actions, as well as the restoration approaches, varied among peatlands: from spontaneous revegetation and passive rewetting driven by beaver activity to active interventions involving surface reprofiling, ditch blocking, and pool excavation. In St Lawrence lowlands, restoration strategies were similarly diverse, including passive rewetting measures (e.g., ditch blocking and berm construction) as well as active approaches such as the Moss Layer Transfer Technique (MLTT) and manual revegetation around pools using fen species. Overall, the restored pools selected were located within fens that had undergone either passive or active restoration at least six years prior to the 2022 vegetation survey, with post-restoration ages ranging from 6 to 35 years. Additional peatland-specific details are provided in Appendix 2.1.

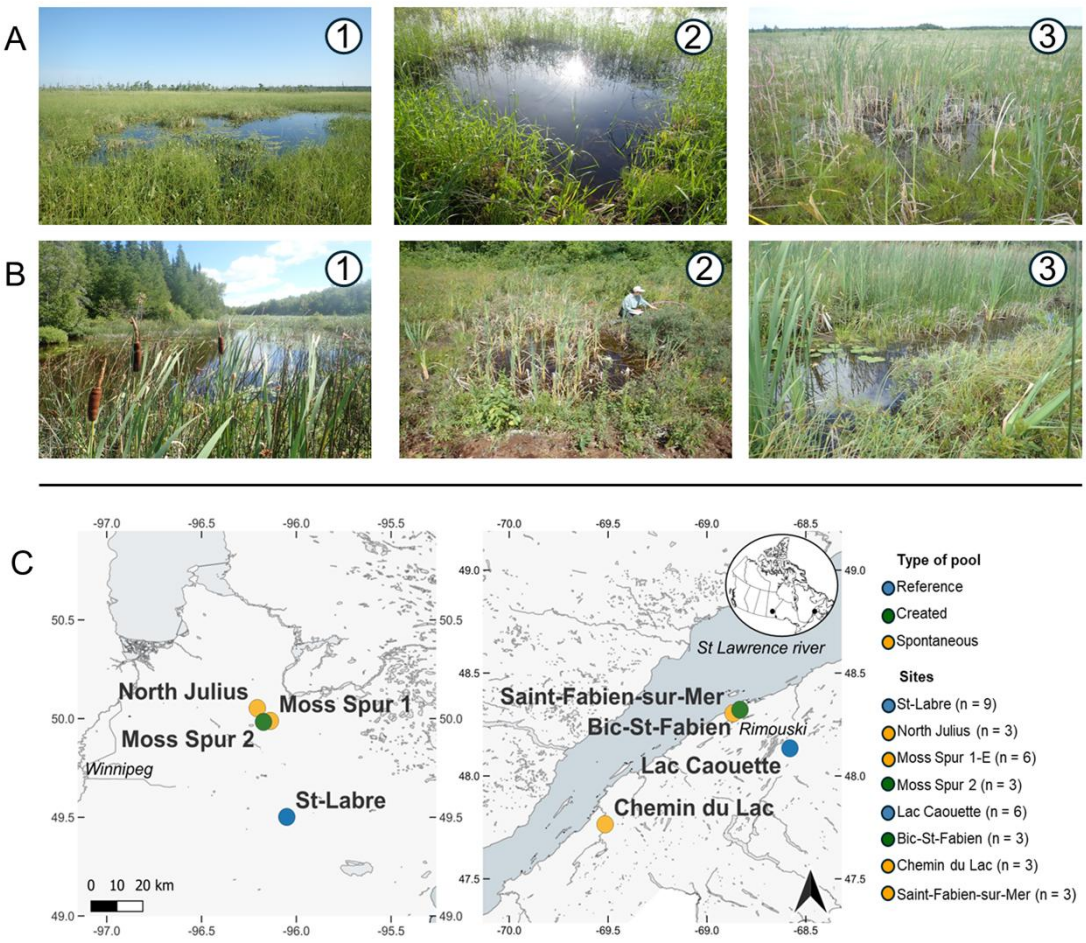

Figure 6. Illustration of the three types of pools [reference (1), created (2), spontaneous (3)] sampled in the Northwestern Forest (A) and St. Lawrence Lowlands climatic region (B). Location of the 36 surveyed pools (C) across eight minerotrophic peatlands (two reference and six restored peatlands in the Northwestern Forest and St. Lawrence Lowlands), with the number of pools indicated in parentheses.

Pool selection

The surface of each peatland was examined using Google Earth satellite imagery (Google Earth, 2023) to locate all visible pools. In both natural reference peatlands, the number of pools was limited; therefore, all existing pools were included in the sampling: nine pools at St-Labre (Northwestern Forest) and six at Lac Caouette (St. Lawrence Lowlands). These pools covered a wide range of dimensions, with depths from 10 to 90 cm and perimeters from 8 to 170 m. In restored peatlands, pool availability was also low, so all pools present on each peatland were sampled. The number of pools per restored peatland varied between 3 and 6. Created pools (n = 6) were distinguished from spontaneous pools (n = 15), which formed unintentionally in wetter depressions or after machinery disturbance.

Vegetation surveys

The vegetation survey around pools was conducted during the summer of 2022 (July to August), following a methodology similar to that used for bogs (Riaño Peña et al., 2026), with four transects placed perpendicularly to the pool margin. In the case of created pools (n = 6), two transects were positioned on the gentle slope and two on the steep slope. In spontaneous (n = 15) and reference pools (n = 15), which generally featured only gentle slopes, four transects were positioned equidistantly around each pools. Along each transect, three 1-m-diameter quadrats were surveyed: the first was placed directly in the water at the pool edge, the second was positioned just outside the standing water at the margin, and the third was located two meters away from the edge. Within each quadrat (n = 432), the cover of different vegetation strata was evaluated, including ericaceous shrubs, other shrubs, herbaceous plants, and bryophytes (comprising liverworts, *Sphagnum* mosses, and *Eubrya* mosses species), with identification carried out at the species level. Plant species that could not be identified in the field were collected and later determined in the laboratory. Nomenclature follows the *Flore des bryophytes du Québec-Labrador* (Faubert, 2012) for liverworts and *Eubrya* species, *Sphagnum Mosses of Eastern Canada* (Ayotte and Rochefort, 2020) for *Sphagnum* species, and *Flora of North America* (Flora of North America Editorial Committee, 1993) and VASCAN, the Database of Vascular Plants of Canada (Brouillet et al., 2010) for vascular plant species.

Vegetation classification

A general classification of vascular plant species was conducted based on their hydric status. For St. Lawrence Lowlands species, the classification followed the *Guide d'identification et de délimitation des milieux humides du Québec méridional* (Lachance et al., 2021), while Northwestern Forest species were classified based on the *National Wetland Plant List Indicator Rating Definitions* (Lichvar et al., 2012). The hydric status of mosses was determined through a comprehensive review of the literature (Faubert, 2012; Lachance et al., 2021; Lemmer et al., 2023; Morin, 2000; Payette and Rochefort, 2001; Vitt, 2014). This classification was conducted to assess the potential of these species to establish typical wetland vegetation after restoration. The established categories were:

- Obligate wetland species (OBL): Species strictly confined to wetlands.
- Facultative wetland species (FACW): Species generally restricted to wetlands.
- Non-indicator species (NI): Species whose presence does not specifically indicate wetland conditions.

Environmental conditions

For each individual pool, a set of common environmental parameters was assessed. The coordinates (longitude, latitude) of each pool were recorded using a GPS tablet equipped with the offline mapping application Avenza

Maps, with a spatial precision of 5–10 meters. The pool perimeter and surface area were estimated using satellite imagery from Google Earth captured during the winter of 2021. The presence of ice on the pool surfaces provided a clearer delineation of their extent in satellite images. Pool depth was determined using a graduated 4-meter string attached to a disk, designed to minimize disturbance to the soft, unconsolidated sediments at the bottom. The pH and electrical conductivity were measured using a pH meter (HI98129, Hanna Instruments) and corrected electrical conductivity (EC) (Sjörs 1950). Additionally, a water sample was collected from each pool between July to August for chemical composition analysis, including total phosphorus (P_{total}), total nitrogen (N_{total}), calcium (Ca), and potassium (K). All samples were stored frozen until analysis. Total phosphorus and total nitrogen were determined following Qualls (1989), while major cations (Ca and K) were extracted according to Amacher et al. (1990) and reported in mg/L (for details, see Figure 2.1).

Statistical analysis

All analyses were performed using R v.4.4.2 (R Core Team, 2022). The variables describing the spatial and environmental conditions of pools included location (longitude, latitude), pool morphology (perimeter of the pool, surface area, depth of the pool), and water chemistry (pH, EC, P_{total}, N_{total}, Ca, K). The type of pool was used as a three-level factor (reference, created, and spontaneous), and the climatic region as a two-level factor (Northwestern Forest and St. Lawrence Lowland). Two sets of vegetation data were analyzed separately: (1) mean total plant cover per quadrat, which was treated as a univariate response, and (2) species composition per pool (n = 36), based on the average cover of each species across the quadrats.

To study variations in species composition between the three types of pool and the two climatic regions, we conducted a PERMANOVA analysis (vegan R-package, Oksanen et al., 2024) with 999 permutations (Anderson and Walsh, 2013), followed by pairwise comparisons for the type of pool (Martinez Arbizu, 2020). Additionally, a PERMDISP analysis with 999 permutations (vegan R package, Oksanen et al., 2024) was performed to assess whether species composition differed within each pool type and climatic region. Both analyses were based on a Hellinger distance matrix, using the mean species cover for each pool. To visualize variations in taxonomic composition among pool types and climatic regions, we used a Non-metric Multidimensional Scaling (NMDS) plot.

To investigate the interaction between the type of pool and the climatic region, a hierarchical clustering analysis was performed. Due to low sample size, this descriptive analysis was considered relevant for highlighting nested patterns in species composition between pools within climatic regions. Hierarchical clustering was conducted on the same Hellinger dissimilarity matrix as previously, using the Ward method, which minimizes intra-cluster variance and promotes the formation of more homogeneous groups (Murtagh and Legendre, 2014). The optimal number of clusters was determined using the gap statistic (factoextra package, Kassambara and Mundt, 2017). Then, to investigate the individual associations of plant species with each cluster, we used the *phi* coefficient of

association (indicspecies R package, De Cáceres and Legendre, 2009), assessing the statistical significance of these associations through permutation tests (n = 999).

To determine the relative influence of each environmental parameter on species composition, we used a distance-based redundancy analysis (db-RDA). To reduce multicollinearity, variance inflation factors (VIFs) were calculated for each predictor, and variables with VIF > 5 were excluded. This analysis was realized by using the same Hellinger dissimilarity matrix as previously. To assess the significance of each environmental parameter, a permutation test (n = 999) was finally conducted.

Results

Variations in plant species composition between the three types of pools and the two climatic regions

Plant species composition varied significantly across the three types of pools (PERMANOVA, $F = 5.8$, $R^2 = 25.9\%$, $p = 0.001$; Figure 7). Pairwise comparisons further confirmed significant differences in plant communities across all pool types (Appendix 2.2). In addition, a significant difference in centroid dispersion among pool types was detected (PERMDISP, $p = 0.034$), indicating varying levels of within-group variability. Dispersion within spontaneous pools (mean distance to centroid = 0.83) was significantly greater than in reference (0.69) and created pools (0.75), suggesting greater compositional heterogeneity within this type of pool. In addition, pool composition differed significantly between the Northwestern Forest: Manitoba and St. Lawrence Lowlands: Quebec (PERMANOVA, $F = 6.19$, $R^2 = 15\%$, $p = 0.001$). This pattern is well represented by the first axis of the NMDS ordination (Figure 7). However, dispersion within groups did not differ between the two climatic regions (PERMDISP, $p = 0.91$).

Based on the hierarchical cluster analysis of pools, the gap statistic identified nine clusters as the optimal number of groups. However, eight clusters were retained because one cluster consisted of a single pool (MS1E-9) and was therefore merged with the nearest cluster, corresponding to spontaneous pools in the Northwestern Forest: Manitoba (MB-Spont 1). The resulting clusters reflected how species composition varied between the two intra-factors, with a greater apparent effect of the type of pool compared to the climatic regions (Figure 8). Specifically, the first and second branches of the dendrogram isolated the reference pools of the Northwestern Forest: Manitoba (MB-ref) and then of the St Lawrence Lowland: Quebec (QC-ref) from the other pools in restored peatlands. The other branches of the dendrogram gradually isolated the created pools (MB-Cr and QC-Cr) from the spontaneous pools (MB-Spont and QC-Spont), with a final distinction based on the climatic region.

The species associated with each cluster are presented according to the hierarchical order of the clustering analysis. Reference pools in both climatic regions (MB-ref and QB-ref) supported more indicator species

spanning several vegetation strata, forbs, graminoids, shrubs, and mosses, almost all of which were associated with obligate wetland (OBL) conditions (Table 4). This contrasted with created pools, where indicator species were fewer and mostly belonged to herbaceous strata (forbs and graminoids), with many taxa showing non-indicator (NI) or FACW hydric statuses rather than strict OBL affinities. Spontaneous pools showed an intermediate pattern: in the Northwestern Forest: Manitoba (MB-Spont), most indicator species were OBL forbs and graminoids, whereas in the St. Lawrence Lowlands: Quebec (QB-Spont), they included a mix of OBL mosses and graminoids, but still fewer strata and hydric types than reference pools.

Table 4. List of plant species significantly associated with the 8 clusters, in minerotrophic peatlands in Northwestern Forest [Manitoba (MB)] and St. Lawrence Lowlands [Quebec (QC)] (based on the phi coefficient of association). For each species, the scientific name (Name), the phi coefficient (phi coef), the p-value, the plant functional type (Group), and the hydric status of the species (Hydric status) are provided.

Cluster Northwestern Forest: Manitoba -Reference pools					
Maianthemum trifolium	*Mai_tri*	0.956	0.001	Forb	OBL
Utricularia vulgaris	*Utr_vul*	0.953	0.001	Forb	OBL
Carex lasiocarpa	*Car_las*	0.945	0.001	Graminoid	OBL
Scorpidium revolvens	*Sco_rev*	0.910	0.001	Moss	OBL
Utricularia intermedia	*Utr_int*	0.903	0.001	Forb	OBL
Scheuchzeria palustris	*Sch_pal*	0.604	0.039	Forb	OBL
Cluster St. Lawrence Lowlands: Quebec-Reference pools					
Schoenoplectus tabernaemontani	*Sch_tab*	0.931	0.001	Graminoid	OBL
Myrica gale	*Myr_gal*	0.906	0.001	Shrub	OBL
Sphagnum girgensohnii	*Sph_gir*	0.871	0.001	Moss	OBL
Comarum palustre	*Com_pal*	0.811	0.001	Forb	OBL
Chamaedaphne calyculata	*Cha_cal*	0.794	0.001	Shrub	OBL
Campylium stellatum	*Cam_ste*	0.680	0.035	Moss	OBL
Calliergon giganteum	*Cal_gig*	0.651	0.025	Moss	OBL
Scorpidium scorpioides	*Sco_sco*	0.622	0.032	Moss	OBL

Straminergon stramineum	*Str_str*	0.602	0.048	Moss	NI
	Cluster Northwestern Forest: Manitoba-Created pools				
Name	***Code sp***	***Phi* Coef**	**p-value**	**Group**	**Hydric status**
Sonchus arvensis	*Son_arv*	0.965	0.002	Forb	NI
Calamagrostis canadensis	*Cal_can*	0.856	0.038	Graminoid	FACW
Equisetum arvense	*Equ_arv*	0.803	0.027	Forb	NI
Phragmites australis	*Phr_aus*	0.801	0.038	Graminoid	FACW
Medicago lupulina	*Med_lup*	0.771	0.022	Forb	NI
Taraxacum officinale	*Tar_off*	0.721	0.044	Forb	NI
Rubus idaeus	*Rub_ida*	0.637	0.022	Forb	NI
	Cluster St. Lawrence Lowlands: Quebec-Created pools				
Sanguisorba canadensis	*San_can*	0.971	0.003	Forb	NI
Spiraea alba	*Spi_alb*	0.942	0.003	Shrub	NI
Gaylussacia baccata	*Gay_bac*	0.813	0.032	Shrub	OBL
Triglochin palustris	*Tri_pal*	0.804	0.030	Forb	OBL
Agrostis scabra	*Agr_sca*	0.761	0.025	Graminoid	NI
Rhynchospora alba	*Rhy_alb*	0.759	0.030	Graminoid	OBL
Euthamia graminifolia	*Eut_gra*	0.758	0.007	Forb	NI
Rhynchospora fusca	*Rhy_fus*	0.756	0.007	Graminoid	OBL
Thuja occidentalis	*Thu_occ*	0.737	0.027	Tree	FACW
Sarracenia purpurea	*Sar_pur*	0.690	0.027	Forb	OBL
	Cluster St. Lawrence Lowlands: Quebec-Spontaneous pools 1				
Typha latifolia	*Typ_lat*	0.98	0.002	Forb	OBL
Spirodela polyrhiza	*Spi_pol*	0.91	0.002	Forb	OBL

	Cluster Northwestern Forest: Manitoba-Spontaneous pools 1				
Trichophorum alpinum	*Tri_alp*	0.981	0.001	Graminoid	OBL
Drosera intermedia	*Dro_int*	0.828	0.002	Forb	OBL
Drosera rotundifolia	*Dro_rot*	0.655	0.018	Forb	OBL
Pogonia ophioglossoides	*Pog_oph*	0.640	0.018	Forb	OBL
Lysimachia thyrsiflora	*Lys_thy*	0.607	0.049	Forb	OBL
	Cluster St. Lawrence Lowlands: Quebec-Spontaneous pools 2				
Carex trisperma	*Car_tri*	0.914	0.001	Graminoid	OBL
Hypericum fraseri	*Hyp_fra*	0.789	0.033	Forb	NI
Warnstorfia fluitans	*War_flu*	0.756	0.027	Moss	OBL
Scirpus cyperinus	*Sci_cyp*	0.754	0.027	Graminoid	OBL
Sphagnum majus	*Sph_maj*	0.747	0.027	Moss	OBL
	Cluster Northwestern Forest: Manitoba-Spontaneous pools 2				
Populus balsamífera	*Pop_bal*	1	0.036	Tree	FACW
Salix bebbiana	*Sal_beb*	0.999	0.036	Shrub	FACW
Populus tremuloides	*Pop_tre*	0.987	0.036	Tree	NI
Salix humilis	*Sal_hum*	0.985	0.036	Shrub	FACW

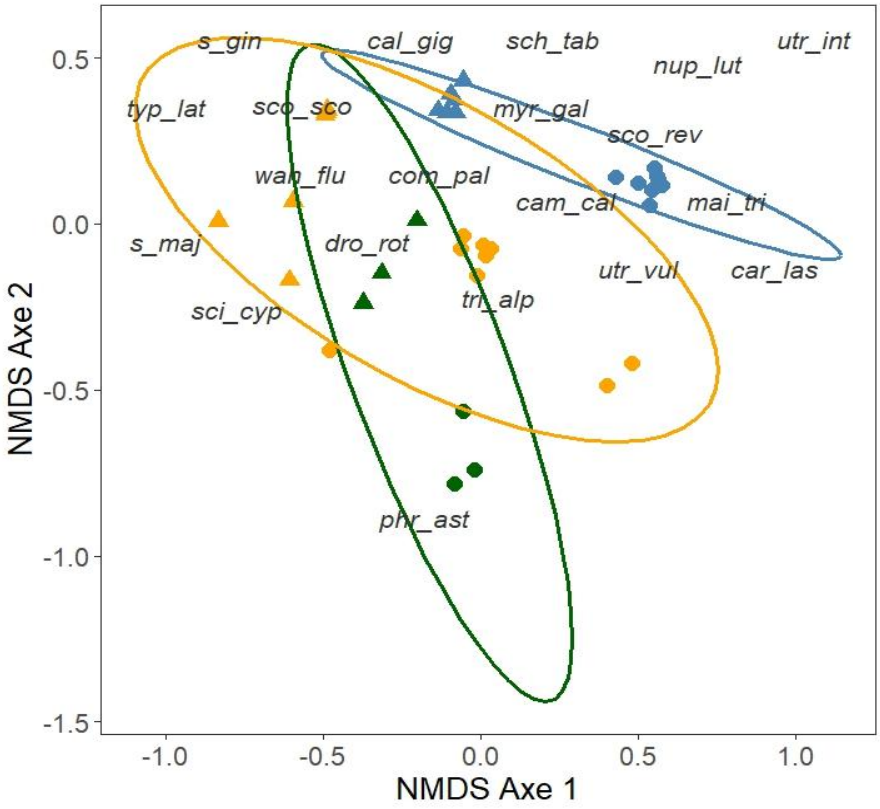

Figure 7. Nonmetric multidimensional scaling (NMDS) ordination plot based on a Hellinger-transformed distance matrix, illustrating differences in plant species composition among the three pool types in minerotrophic peatlands of the Northwestern Forest [Manitoba (MB)] and St. Lawrence Lowlands [Quebec (QC)] climatic regions (Appendix 2.1). The ordination was generated using the *metaMDS* function and is intended for visualization only. Only the scores of the 20 most abundant species are shown (full species names are provided in Table 1). Statistical differences in species composition among pool types and regions were independently tested using PERMANOVA, while differences in multivariate dispersion were assessed using PERMDISP. These analyses are complementary but not directly linked to the NMDS ordination.

For each cluster of pools (Figure 8), variations in the mean values of environmental variables provided a descriptive characterization of their abiotic conditions (Table 5). Reference pools were characterized by nutrient-poor and neutral to slightly basic conditions, typical of stable, less disturbed environments (MB-Ref and QC-Ref). Created pools showed contrasting characteristics between regions: those in the Northwestern Forest reflected minerotrophic conditions with deeper water and higher conductivity and calcium (MB-Cr), whereas those in St. Lawrence Lowlands were more acidic and nutrient-enriched, particularly in nitrogen (QC-Cr). Spontaneous pools exhibited the greatest environmental variability. St. Lawrence Lowlands sub-group 2 displayed conditions indicative of mineral influence, with elevated phosphorus concentrations (QC-Spont2), while its Northwestern Forest counterpart was associated with low calcium and nitrogen (MB-Spont2). In contrast, St. Lawrence Lowlands sub-group 1 was characterized by low electrical conductivity and calcium (QC-Spont1), and Northwestern Forest sub-group 1 by acidic, nutrient-rich waters (MB-Spont1).

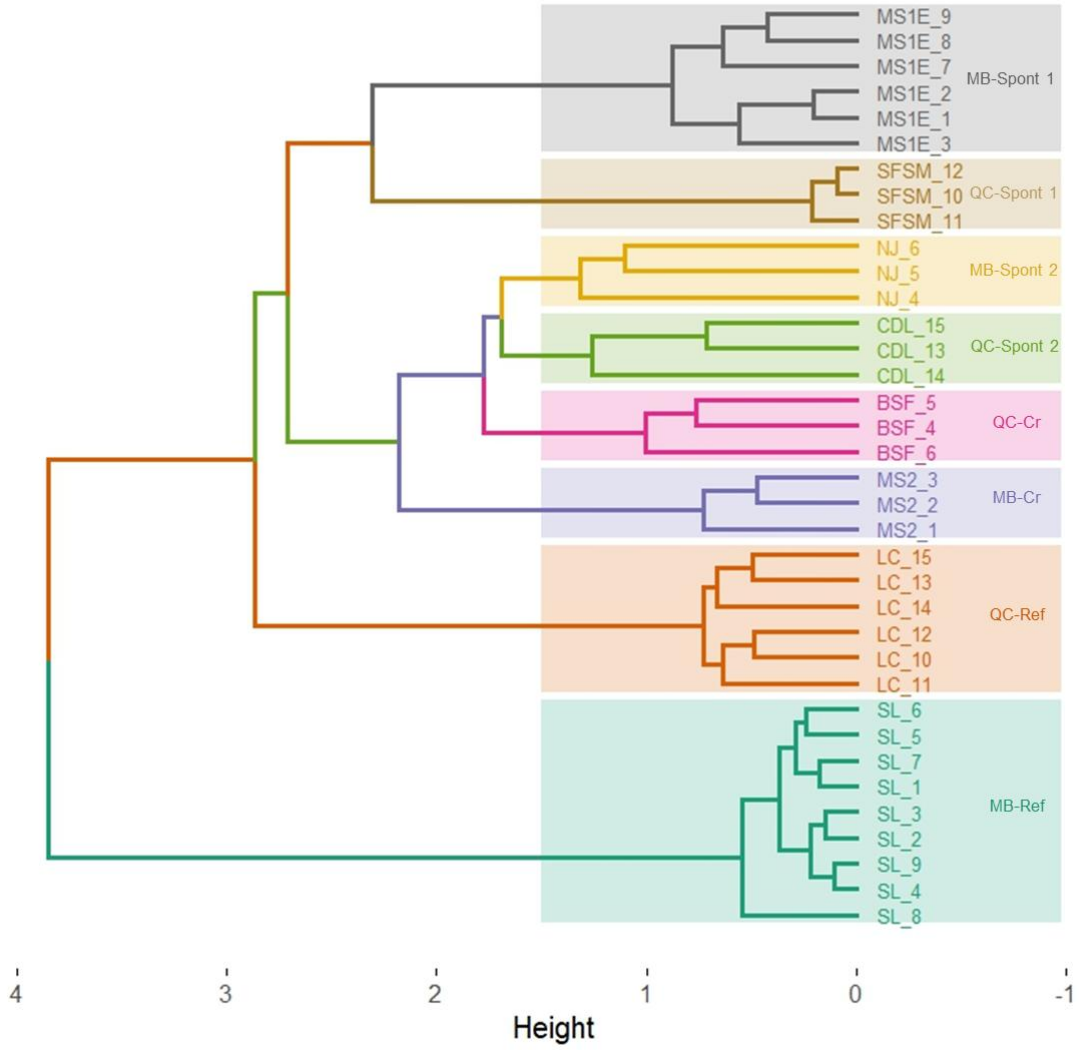

Figure 8. Ascendant hierarchical classification performed between the three types of pools (Reference = Ref, Created = Cr, Spontaneous = Spont) in minerotrophic peatlands in the Northwestern Forest [Manitoba (MB)] and St. Lawrence Lowlands [Quebec (QC)], full site names are provided in Appendix 2.1.

Table 5. Variations in morphological and chemical conditions (mean ± standard deviation [SD]) between the 8 clusters in minerotrophic peatlands in the Northwestern Forest [Manitoba (MB)] and the St. Lawrence Lowlands [Quebec (QC)].

Cluster	Province	Pool type	Depth pool (cm)	Perimeter (m)	pH	EC (µS/cm)	Total phosphorus (Ptotal, mg/L)	Total nitrogen (Ntotal, mg/L)	Potassium (K, mg/L)
MB-Ref	Manitoba	Reference	68 ± 17	68 ± 44	7 ± 0.3	266 ± 31	0.05	0.5 ± 0.1	0.3 ± 0.2
MB-Cr	Manitoba	Created	75 ± 15	33 ± 42	6.8 ± 0.1	331 ± 99	0.1 ± 0.02	2.1 ± 0.4	0.7 ± 0.2
MB-Spont 1	Manitoba	Spontaneous	42 ± 27	28 ± 10	5.7 ± 0.8	141 ± 38	0.1 ± 0.06	3 ± 1	1.7 ± 0.5
MB-Spont 2	Manitoba	Spontaneous	51 ± 19	23 ± 10	5.9 ± 0.3	68 ± 24	0.08 ± 0.02	1 ± 0.2	0.7 ± 0.5
QC-Ref	Quebec	Reference	45 ± 10	39 ± 16	7 ± 0.3	178 ± 60	0.07 ± 0.02	0.6 ± 0.1	0.6 ± 1
QC-Cr	Quebec	Created	18 ± 10	15 ± 3	6 ± 0.1	138 ± 87	0.1 ± 0.06	5 ± 3	2 ± 1
QC-Spont1	Quebec	Spontaneous	40 ± 26	12 ± 1	6 ± 0.3	50 ± 12	0.07 ± 0.01	1.5 ± 0.3	0.7 ± 0.5
QC-Spont 2	Quebec	Spontaneous	55	12 ± 2	6 ± 0.2	141 ± 16	0.3 ± 0.2	3 ± 1	2 ± 0.6

Relative influence of environmental parameters on species composition

Species composition differed among pools in relation to measured environmental variables, indicating a strong ecological influence of the measured variables (db-RDA: 38.7% of explained variation, F = 3.45, p = 0.001; Figure 9). Among these 10 variables, nine significantly contributed to differences in taxa composition among pools, with longitude (20%, p = 0.001), pool water calcium concentration (17.7%, p = 0.002), electrical conductivity (13.5%, p = 0.003), total phosphorus (11%, p = 0.001), and total nitrogen (10%, p = 0.033) emerging as the most influential (Appendix 2.3).

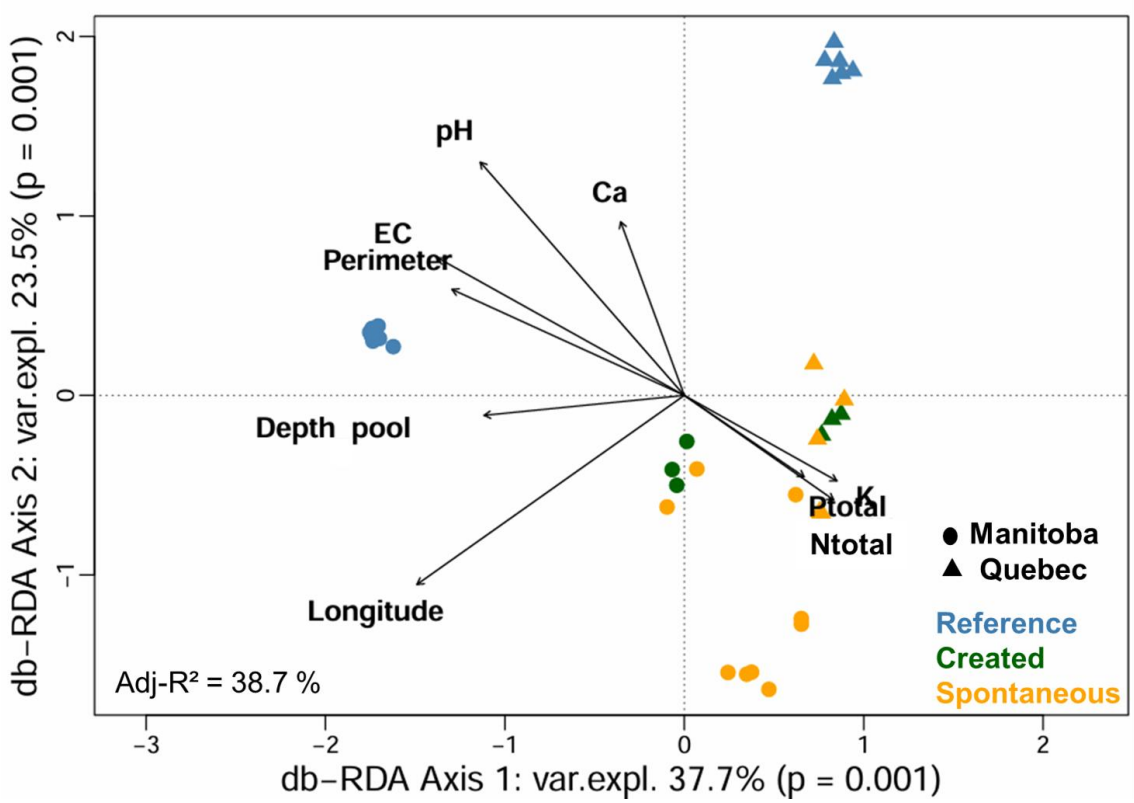

Figure 9. Distance-based redundancy analysis (db-RDA) of the Hellinger distance matrix of plant communities concerning spatial, morphological, and chemical variables between the three types of pools in minerotrophic peatlands in Northwestern Forest [Manitoba (MB)] and St. Lawrence Lowlands [Quebec (QC)] (Adj-R^2 = adjusted-R^2, i.e., proportion of variation in species composition explained by environmental parameters; var.expl = variance explained by axes 1 and 2, see Appendix 2.3 for more details).

Discussion

This study investigates variations in species composition in aquatic habitats within restored, moderately rich fens, focusing on created and spontaneous pools distributed across two distinct climatic regions. By comparing

these pools to natural reference pools, we reveal significant differences in community structure. Species composition differed significantly both between pool types and climatic regions; however, their relative influence was not equivalent. Pool type emerged as the primary driver of variation, with reference pools forming more distinct assemblages than created and spontaneous pools across both regions. In contrast, the effect of climatic region was more nuanced and depended on pool type, being particularly pronounced in reference pools while comparatively weaker in created and spontaneous pools. These results suggest that, when planning peatland pool restoration, the selection of species to reintroduce should primarily rely on appropriate reference ecosystems, while also accounting for regional context. Overall, the stronger influence of pool type over climatic region highlights the importance of local habitat conditions in structuring plant communities, although regional factors still modulate these patterns, especially in less disturbed systems.

How does species composition vary across reference pools between the two climatic regions?

Reference pools located in the Northwestern Forest climatic region differed markedly from reference pools located in the St Lawrence Lowland, in terms of species composition. For example, six species obligate to wetlands were associated with reference pools in the Northwestern Forest, with five species exhibiting a *phi* coefficient above 90%, indicating their uniqueness of these species associated with these pools (*Maianthemum trifolium, Utricularia vulgaris, Carex lasiocarpa, Scorpidium revolvens, U. intermedia*). Most of these species revealed by the *phi* coefficient were vascular, even though bryophytes generally dominate fen diversity in peatland pools (Vitt et al., 1995). The presence of carnivorous species such as *Utricularia vulgaris* and *U. intermedia*, typically associated with pools or open water, was restricted to the Northwestern Forest climatic region. Generally, in natural fens, plant communities are structured into five dominating functional layers: trees, shrubs, graminoids (sedges, grasses, and rushes), forbs, and bryophytes (Frolking et al., 2011; Hassanpour Fard et al., 2020; Robroek et al., 2015; Ward et al., 2009). Results from the *phi* coefficient revealed that forbs and graminoids are more closely associated with reference pools in the Northwestern Forest, while bryophytes are more characteristic of reference pools in St Lawrence lowlands (*Sphagnum girgensohnii, Campylium stellatum, Calliergon giganteum, Scorpidium scorpioides, Straminergon stramineum*). This difference may reflect how regional environmental conditions, in particular nutrient availability and hydrological regimes, shape the specificity of bryophyte communities to reference pools. In the Northwestern Forest, higher nutrient availability or more variable hydrology may allow common bryophyte species to occur across both reference and restored pools, reducing their distinctiveness in reference sites. In contrast, in the St. Lawrence Lowlands, lower nutrient levels and more stable hydrological conditions may favour bryophyte species that are more tightly associated with reference pools, thereby increasing their specificity (Bubier, 1995; Turmel-Courchesne et al., 2023).

Species composition between reference pools in the Northwestern Forest and St. Lawrence Lowland reflects the well-documented regional divergence in peatland species (Warner and Asada, 2006; Glaser et al., 2004). Importantly, these regional differences persist in restored pools (created and spontaneous), even though some widespread taxa, such as *Typha*, which is indeed an indicator of spontaneous pools in the St. Lawrence Lowlands, could have been expected to promote a certain degree of homogenization across regions (Bansal et al., 2019; Wilcox et al., 2018). This suggests that vegetation recolonization in restored pools is strongly constrained by the regional species pool, rather than being driven by uniform colonization dynamics (Galatowitsch, 2006; Zobel et al., 1998).

Species composition in both created and spontaneous pools remained distinct from reference pools, indicating that restoration efforts have not yet reproduced the characteristic assemblages of reference peatland pools (Jolin et al., 2024). Both types of restored pools, therefore, reflect the ecological distance that still separates them from reference ecosystems, whether they were actively restored (created) or passively colonized (spontaneous pools). Similar distinctions between natural and restored sites have been noted in other wetland systems, such as prairie potholes (Galatowitsch and Van der Valk, 1996), and vernal pools in California (Collinge et al., 2013), where restoration efforts often fail to fully replicate reference community composition. The spontaneous pools exhibited the highest dispersion, indicating greater compositional heterogeneity than the created and reference pools. This greater heterogeneity in spontaneous pools may reflect a wider range of colonization pathways, microhabitat variability, or successional stages (Alderson et al., 2019; Beadle et al., 2015; Jolin et al., 2024; Larkin et al., 2016). It could also indicate more stochastic community assembly processes without active restoration design (Måren et al., 2018; Trowbridge, 2007).

Plant colonization in restored fens is strongly influenced by post-restoration hydrological conditions and the time elapsed since restoration (Lamers et al., 2015). In our studied peatlands, restoration was primarily achieved through rewetting and spontaneous passive revegetation. However, peatlands that received active plant reintroduction also experienced spontaneous colonization. In the created pools of the Northwestern Forest climatic region, we observed two facultative wetland species (*Calamagrostis canadensis, Phragmites australis*) and five non-indicator species (*Sonchus arvensis, Equisetum arvense, Medicago lupulina, Taraxacum officinale, Rubus idaeus*), reflecting possibly early successional conditions and suboptimal hydrological conditions that favoured generalist pioneer and ruderal species (Büchi and Vuilleumier, 2014; Muench and Elsey-Quirk, 2019). This may be partly due to the widespread spontaneous revegetation that followed rewetting, which, as Gagnon et al. (2018) observed at the Moss Spur site, allows colonization under variable post-restoration environmental conditions, favouring a broader range of species and contributing to higher local diversity (Šebelíková et al., 2016; Tischew et al., 2014). Limited plant presence and the scarcity of viable seed banks in the residual peat and adjacent bog areas (Campbell et al., 2003; Poulin et al., 1999; Salonen, 1994) further constrain

recolonization. In the St. Lawrence Lowlands created pools, we identified five obligate wetland species (*Gaylussacia baccata, Triglochin palustris, Rhynchospora alba, Rhynchospora fusca, Sarracenia purpurea*), one facultative species (*Thuja occidentalis*), and four non-indicator species (*Sanguisorba canadensis, Spirea alba, Agrostis scabra, Euthamia graminifolia*). These pools hosted more ombrotrophic species, such as *G. baccata*, *R. alba*, and *S. purpurea*, likely due to more acidic water conditions than those in the reference pools. In Finland, Haapalehto et al. (2011) also found that even a decade after fen rewetting, many minerotrophic species remained absent, with generalist ombrotrophic species still dominating. Unique species like carnivorous species, i.e., *Utricularia sp.*, typically associated with pools or open water, were absent from all restored pools. This absence is unlikely to result solely from pH or dispersal constraints (Prausová et al., 2022; Sirová et al., 2003), since *Utricularia* have also been reported in restored sites with more acidic waters and limited hydrological connectivity (Fontaine et al., 2017; Lovadi et al., 2023). Rather, the absence of permanent water in restored pools can be a primary factor limiting the establishment of *Utricularia* spp. in both created and spontaneous pools (Adamec, 2020). Water level fluctuations can also influence vegetation establishment (Slack et al., 1980). For example, in western Alberta, *Scorpidium scorpioides* was found to thrive in very wet conditions but was intolerant to drier ones, often being replaced by *Scorpidium revolvens* as conditions became less saturated, indicating a shift in vegetation composition driven by hydrological change. Although the water table was not directly measured in this study, *Scorpidium scorpioides* and *Scorpidium revolvens* were found exclusively in reference pools in both Quebec and Manitoba, where water levels are relatively stable due to undrained natural conditions. In contrast, created and spontaneous pools are likely subject to greater water table fluctuations, common in restored peatlands (Holden et al., 2018), which may hinder the establishment of these species.In the Northwestern forest climatic region, the spontaneously formed pool with greater depth, lower conductivity, and low nutrient concentrations (MB-Spont1) supported obligate wetland species such as *Drosera intermedia*, *D. rotundifolia*, and *Trichophorum alpinum*, taxa generally associated with acidic substrates and stable water tables (Fontaine et al., 2017; Jones et al., 2016). When the spontaneously formed pools were shallower and associated with higher electric conductivity (greater minerotrophy) and nutrient levels (MB-Spont2), they harboured more facultative or even non-indicator species, such as *Populus balsamifera* and *Salix bebbiana*. The richer conditions may stem from higher water table level fluctuations in shallow pools, potentially driven by drought and rewetting cycles, which enhance peat decomposition and thus increase nutrient concentrations (Arsenault et al., 2019).

In the St. Lawrence Lowlands climatic region, a similar dichotomy was observed. Deeper spontaneously formed pools with associated elevated nutrient and sodium concentrations (QC-Spont2), favoured obligate competitive species such as *Typha latifolia* and *Spirodela polyrhiza*. These species can strongly influence community assembly by limiting the establishment of other taxa (Meeker et al., 2023; Wilcox et al., 2018). In particular, *Typha latifolia* can reduce bryophyte cover and form monotypic stands (Grace and Wetzel, 1981; Graf et al., 2008; Hartsock et al., 2021). On the other hand, shallower spontaneous pools with more acidic conditions that

resembled reference pools (QC-Spont1) were characterized by typical wetland plants such as *Carex trisperma*, *Warnstorfia fluitans*, *Scirpus cyperinus*, *Sphagnum majus*, and *Hypericum fraseri*. Contrary to *Typha* species, *S. cyperinus* supports more associated species and decomposes slowly, enhancing peat accumulation potential (Graf and Rochefort, 2009). Overall, the higher number of species associated with pools in the St. Lawrence Lowlands climatic region (all types combined) (30 species) compared to those in the Northwestern forest (22 species), with more bog-associated plants such as *Sarracenia purpurea* and *Chamaedaphne calyculata*, indicates stronger wetland affinities in this region. This pattern suggests that hydrological conditions, reflected by water levels and saturation patterns, play a key role in supporting a broader range of wetland species, which may reflect interactions between local abiotic conditions and broader climatic gradients (Jean and Bouchard, 1993). When considering only restored pools (both created and spontaneous), St. Lawrence Lowlands hosted more obligate and facultative wetland species (16) than the Northwestern forest (10), highlighting ecological differences between climatic regions and the need for restoration approaches adapted to local conditions.

Which environmental parameters shape species composition?

Longitude played a crucial role in determining species composition between pools in the Northwestern Forest and St. Lawrence Lowlands climatic regions. For example, reference pools located at St. Lawrence Lowlands in the Bas-St-Laurent region (Quebec) were characterized by higher concentrations of sodium, being more exposed to events of sea spray deposits (Comeau and Bellamy, 1986). Although biogeographical differences appeared to have a strong influence (RDA analysis), likely due to climatic or site-specific factors, pool type played a more critical role in shaping community structure. Each pool type may have created distinct environmental conditions, such as differences in water table stability, depth, or substrate composition, influencing species distribution. However, the environmental variations observed between pools (Table 2) remained subtle, indicating that repeated monitoring of hydrological conditions and water chemistry across multiple seasons, rather than a single summer sampling, would be needed to better disentangle the effects of climate from local site characteristics.

Electrical conductivity values were generally higher in the Northwestern forest climatic region than in the St. Lawrence Lowlands across both reference and created pools, which may have contributed to the observed differences in species composition. Phosphorus and nitrogen concentrations were similar between climatic regions. Increased phosphorus availability can promote the growth and colonization of species with high nutrient demands, favouring vascular plants over bryophytes (Arsenault et al., 2018; Chee and Vitt, 1989; Verhoeven et al., 1990). For example, spontaneous pools in the St. Lawrence Lowlands were primarily colonized by *Typha latifolia*.

Implications for restoration

The findings of our study provide a first insight into practical guidance for the restoration of minerotrophic pools in two distinct climatic regions of Canada: the Northwestern Forest and the St. Lawrence Lowlands. Our results indicate that the active reintroduction of plants is necessary to achieve the establishment of target vegetation in restored pools (Fontaine et al., 2017; Laberge et al., 2013). However, reintroduction efforts should consider the regional context, as differences were observed in the species associated with reference peatland pools between the two climatic regions. It should be noted that only one reference site per region was included in this study, and thus, these differences may partly reflect site-specific characteristics. Nevertheless, each reference site was selected as representative of the typical conditions of its region, providing some basis for regional interpretation. In the Northwestern Forest, priority species for reintroduction include *Maianthemum trifolium*, *Scorpidium revolvens*, *Utricularia vulgaris*, and *Utricularia intermedia*, whereas in the St. Lawrence Lowlands, species such as *Schoenoplectus tabernaemontani*, *Myrica gale*, and *Scorpidium scorpioides* should be targeted. In minerotrophic fens, water chemistry, particularly calcium, phosphorus, and nitrogen concentrations, was associated with patterns of vegetation establishment across pools, whereas pool morphology (perimeter and depth) did not show a significant effect. This contrasts with vegetation patterns reported for ombrotrophic pools, where pool morphology can strongly influence vegetation composition through its effects on light penetration, water temperature, and biogeochemical processes (Jolin et al., 2024; Riaño Peña et al., 2026). These results suggest that abiotic conditions related to water chemistry may play a greater role than pool morphology in structuring vegetation communities in minerotrophic pools. Although differences in vegetation composition among pool types may reflect underlying differences in hydrological conditions, no direct measurements of water table dynamics, hydroperiod, or water-level fluctuations were collected in this extensive spatial study. Consequently, the role of hydrology cannot be directly assessed and should be considered a hypothesis requiring further investigation. Future restoration studies would benefit from long-term hydrological monitoring to determine how water-level dynamics interact with water chemistry to influence the establishment and persistence of characteristic minerotrophic pool species such as Utricularia spp. and *Scorpidium* spp. Overall, our results highlight the importance of considering regional species pools and local water chemistry when restoring minerotrophic peatland pools. Further research integrating vegetation, hydrological, and physicochemical monitoring will be necessary to identify the environmental conditions that most effectively promote the recovery of reference-like plant communities.

Appendices

Table 2. 1. List of sites and sectors where pools were sampled by province (the Northwestern Forest [Manitoba (MB)] and the St. Lawrence Lowlands [Quebec (QC)]) for the three types of pools in the minerotrophic peatlands (reference [n = 15], created [n = 6], spontaneous [n = 15]). The table provides the peatland names, sector locations, restoration types, and restoration years.

							Types of pools		
Climatic regions	**Site and sector**	**Code site**	**Latitude, longitude**	**Type of interventions**	**Year of cessation of peat extraction**	**Year of restoration**	**Reference**	**Created**	**Spontaneous**
Northwestern Forest (Manitoba)	Moss Spur 1-E	MS1E	49.9886 N, -96.1371 W	Spontaneous revegetation	1995	-	0	0	6
	North Julius	NJ	50.0531 N, -96.2058 W	Spontaneous revegetation	2012	-	0	0	3
	St-Labre	SL	49.5020 N, -96.0504W	-	--	-	9	0	0
	Moss Spur 2	MS2	49.9835 N, -96.1733 W	Surface reprofiling, natural rewetting driven by beavers, and excavation of pools	1999	2019	0	3	0
St. Lawrence Lowlands (Quebec)	Saint-Fabien-sur-Mer-D	SFSM	48.3048 N, -68.8679 W	Rewetting and surface reprofiling	1999	2011	0	0	3
	Chemin du Lac	CDL	47.7652 N, -69.5151 W	Rewetting	1995	2004	0	0	3
	Lac Caouette	LC	48.1347 N, -68.5806 W	-	-	-	6	0	0
	Bic-St-Fabien	BSF	48.3220 N, -68.8332 W	Fen moss transfer, rewetting, surface profiling, excavation of pools	1990	2009/2010	0	3	0

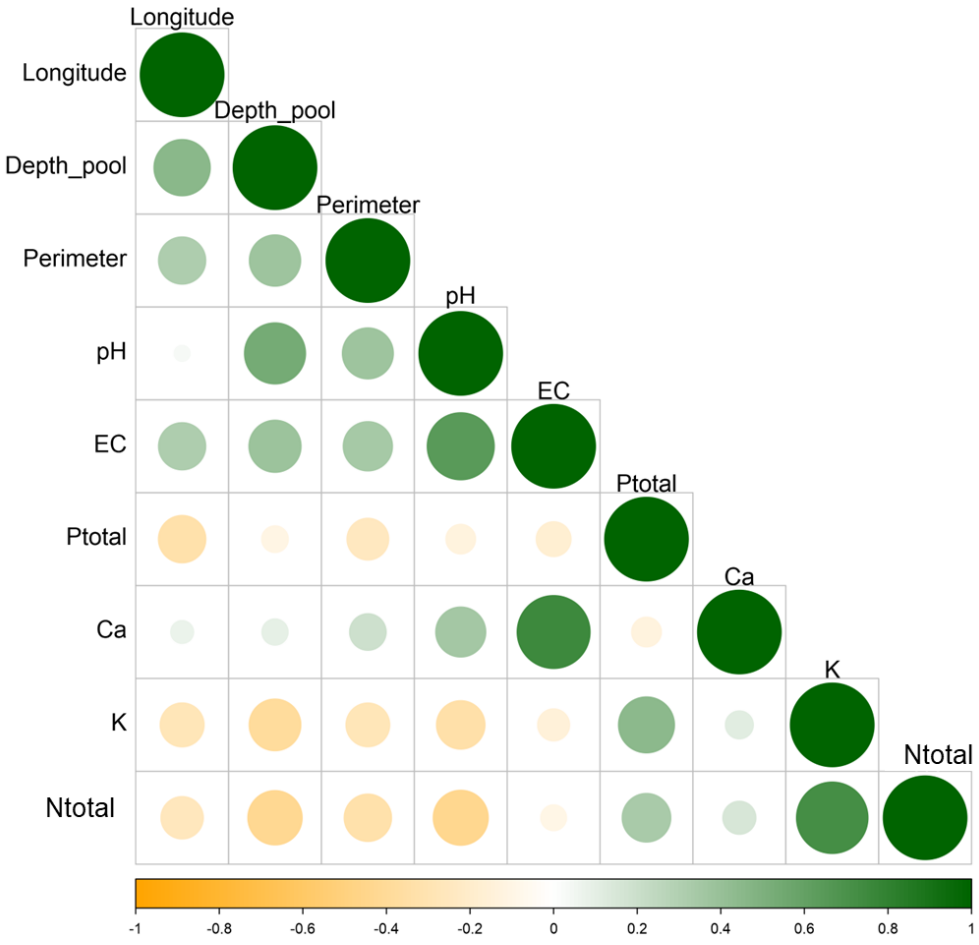

Figure 2. 1. Correlation matrix of the environmental conditions: longitude, depth pool, perimeter, pH, electrical conductivity (EC), total phosphorus (P_{total}), calcium (Ca), potassium (K), total nitrogen (N_{total}), used to describe variations in species composition for the three type of pools in the minerotrophic peatlands (reference [n = 15], created [n = 6], spontaneous [n = 15]), in the Northwestern Forest [Manitoba (MB)] and the St. Lawrence Lowlands [Quebec (QC)].

Table 2. 2. Results for the PERMDISP analysis between the three types of pools (reference [n = 15], created [n = 6], spontaneous [n = 15]) in the minerotrophic peatlands located in the Northwestern Forest [Manitoba (MB)] and the St. Lawrence Lowlands [Quebec (QC)]. The p-value is the p-value for each pairwise comparison, and finally, p-adjusted is the adjusted p-value, which corrects for multiple comparisons.

Comparison	Df	Sum of squares (SS)	F value	R2	p-value	p-adjusted
Created vs Reference	1	3.61	6.29	0.24	0.001	0.0015
Created vs Spontaneous	1	2.22	3.01	0.13	0.003	0.0030
Reference vs Spontaneous	1	4.95	7.65	0.21	0.001	0.0015

Table 2. 3. Results for the db-RDA analysis for each environmental variable used to predict plant composition between the three types of pools (reference [n = 15], created [n = 6], spontaneous [n = 15]) in the minerotrophic peatlands situated in the Northwestern Forest [Manitoba (MB)] and the St. Lawrence Lowlands [Quebec (QC)].

Variables	**Df**	**Variance**	**F**	**Pr(>F)**	**% Intrinsic**	**% Total (constrained)**
Longitude	1	1.9	3.74	0.001	**20.04**	11.99
Calcium	1	1.68	3.3	0.003	**17.72**	10.61
Electrical conductivity	1	1.28	2.52	0.007	**13.50**	8.08
Total phosphorus	1	1.01	1.99	0.015	**10.65**	6.38
Total nitrogen	1	0.97	1.91	0.033	**10.23**	6.12
pH	1	0.78	1.53	0.116	**8.23**	4.92
Perimeter	1	0.77	1.52	0.121	**8.12**	4.86
Depth pool	1	0.72	1.41	0.152	**7.59**	4.55
Potassium	1	0.37	0.72	0.754	**3.90**	2.34
Residual	26	13.23				
Constrained	9	9.48			**100**	

Chapitre 3 Divergent plant recovery along a hydrological gradient in restored *Sphagnum*-dominated peatland pools

3.1 Résumé

Les mares des tourbières sont des microformes clés pour la biodiversité. L'extraction de la tourbe les dégrade en éliminant la végétation et en drainant les sites. Cette étude, réalisée dans l'est du Canada, compare la composition végétale de 26 mares de référence et de 41 restaurées dans des tourbières à sphaignes, le long d'un gradient hydrologique (0, 1, 2 et 10 m de la mare). Les tourbières restaurées sont classées en jeunes (6 – 13 ans) et anciennes (15 – 26 ans) et incluent des mares créées et spontanées. La richesse et la composition varient le long du gradient hydrologique, perpendiculairement à la mare. Les mares créées gagnent en richesse mais restent dominées par des espèces généralistes. Les mares spontanées, moins riches, sont plus proches des communautés de référence. Une richesse élevée ne reflète pas une meilleure restauration des communautés cibles, qui dépend surtout des conditions favorisant les espèces spécialistes et les gradients hydrologiques progressifs.

3.2 Abstract

Peatland pools are key microforms within the ecosystem that support specialized plant biodiversity. Peat extraction disrupts these ecosystems through vegetation removal and drainage, often leading to the complete loss of pools. This study, conducted in eastern Canada, compares vegetation composition in 26 reference pools from undisturbed peatlands with 41 pools in restored Sphagnum-dominated peatlands along a perpendicular hydrological gradient (distances 0, 1 m, 2 m and 10 m from the pool). Restored peatlands were grouped by time since restoration into young (6 – 13 years) and old (15 – 26 years) peatlands and included two pool types: created and spontaneous. Compared with reference pools, restored pools showed differences in community structure across all pool types. Plant species richness and composition varied along the perpendicular hydrological gradient across all pool types, highlighting the importance of the hydrological gradient in shaping distinct species assemblages and contributing to overall diversity in Sphagnum-dominated peatlands (Malhotra et al., 2016). In created pools, species richness increased with time and became closer to that of reference pools. However, species composition did not follow the same trend: at intermediate and distant positions along the gradient, communities remained dominated by generalist or non-target pool species such as Typha latifolia. In contrast, spontaneous pools supported lower species richness but showed composition more similar to reference pools, including the presence of characteristic species such as

Sphagnum fallax. Across restored pools, higher species richness did not necessarily indicate a closer recovery of target peatland communities with time. Management strategies should therefore focus not only on enhancing colonization, but also on promoting conditions that favour pool specialists. Adjusting microtopography to create more gradual hydrological transitions and improving propagule availability may help steer community assembly toward reference conditions.

Keywords: ecological restoration, water bodies, aquatic plant species, *Sphagnum*-dominated peatlands, vegetation composition, hydrological gradient.

Introduction

Pools are a common feature of northern peatlands (Glaser and Janssens, 1986) and form a type of microform, defined as small-scale structural elements that characterize peatland landscapes (Lindsay, 2010; Beadle et al., 2015). In natural peatlands, pools are widely recognized as biodiversity hotspots because they provide key conditions or resources that support diverse plant and animal species (Dibner et al., 2014; Fontaine et al., 2007; Mazerolle et al., 2006; Verberk et al., 2006). In ombrotrophic peatlands (bogs) of the boreal zone in North America, pools are typically dominated by *Sphagnum* species, mainly from the Cuspidata subgenus, such as *Sphagnum majus* and *Sphagnum cuspidatum*. These species are often associated with extensive liverwort carpets, including *Odontoschisma fluitans, Gymnocolea inflata* and *Mylia anomala*, as well as vascular plants like *Carex limosa*, *Scheuchzeria palustris*, and *Utricularia cornuta* (Fontaine et al., 2007; Riaño Peña et al., 2026). Together, these communities increase the structural complexity of peatland pools and contribute to their ecological significance.

In North America, horticultural peat extraction affects only a subset of bog peatlands (Poulin et al., 2004), yet its strong spatial concentration, particularly in Eastern Canada, can result in substantial regional reductions of bog area and associated habitats (Joosten and Clarke, 2002; Pellerin and Poulin, 2013). These disturbances contribute to the loss of bog pools, primarily through drainage-induced hydrological alterations (Holden, 2004; Holden et al., 2006; Price, 2003), with cascading effects on biodiversity that extend beyond plant communities to multiple trophic groups. In addition, processes such as frost heaving (Groeneveld and Rochefort, 2002; Groeneveld and Rochefort, 2005), soil erosion (Campbell et al., 2002; Nugent et al., 2003; Tuukkanen et al., 2014), and depletion of the peatland seed bank (Graham and Page, 2018; Janzen and Vázquez-Yanes, 1991) further constrain vegetation recovery and reduce the resilience of peatland ecosystems following pool loss. Ecological restoration of bogs aims to reverse the impacts of anthropogenic disturbance by re-establishing ecological processes necessary for long-term ecosystem functioning and service provision (Gann et al., 2019). In Canada, bog restoration efforts primarily target the recovery of carbon sequestration by reinstating peat-forming vegetation and hydrological conditions (Harris et al., 2022; Mander et al., 2024; Nugent et al., 2019),

most commonly through the application of the Moss Layer Transfer Technique (MLTT) (Rochefort et al., 2003; Graf and Rochefort, 2016). This approach involves spreading donor material, composed mainly of *Sphagnum* fragments and companion bryophytes, over the residual peat surface. The technique is combined with topographic interventions such as berm construction, blocking drainage ditches, and peat surface freshening (Quinty et al., 2019, 2020a, b, c; Rochefort et al., 2003). Although MLTT enables the re-establishment of bog plant communities within approximately 5 to 10 years (Gonzáles et al., 2014; Liu et al., 2024), the technique primarily targets peatland surfaces and does not specifically address the distinct ecological and hydrological requirements of pool habitats. This leaves pool margins largely dependent on spontaneous recolonization and on the regional availability of pools as propagule sources, a context that offers limited prospects for effective recovery and therefore warrants further investigation.

Pools may be actively created during restoration following recommendations outlined in the *Peatland Restoration Guide* (Quinty et al., 2020a, b), which define parameters related to pool morphology but do not include a standardized approach for plant reintroduction in pools. Shallow pools can also form spontaneously, where water accumulates in depressions created by machinery or in naturally low-lying areas (Riaño Peña et al., 2026). Within restored ombrotrophic peatlands, pools are created with empiric configurations, resulting in diverse environmental conditions, but are usually structured with a pronounced perpendicular gradient from the pool centre toward the margins. This gradient reflects a progressive decrease in water table depth and flooding duration, accompanied by increasing substrate stability and a growing influence of surrounding vegetation matrix, including both *Sphagnum* carpets and vascular plants established farther from the pool edges. Together, these factors generate fine-scale hydrological and physical gradients (Xu et al., 2015; Qi et al., 2021; Raulings et al., 2010). In restored peatlands, pools develop perpendicular hydrological and microtopographic gradients that act as abiotic filters shaping plant establishment. These gradients constrain species establishment based on their tolerance to inundation and substrate instability (Butterfield and Palmquist, 2024; Pellerin et al., 2009; Wang et al., 2025), and steeper gradients are expected to support lower species diversity due to reduced niche availability, although this has not been explicitly tested in peatland pools.

The gradients are initially poorly defined and embedded within highly unstable hydrological and physical conditions. Water levels tend to fluctuate widely (Haapalehto et al., 2011; Whittington and Price, 2006), and substrates remain unconsolidated, limiting plant establishment and favouring sparse or pioneer vegetation (Laberge et al., 2015; Landry et al., 2012; Pouliot et al., 2011). Over time, hydrological conditions stabilize, substrates consolidate, and biotic interactions, such as facilitation and competition, intensify, leading to more structured plant communities (Malhotra et al., 2016; Bruland and Richardson, 2005). As a result, the ecological influence of perpendicular gradients on vegetation is expected to strengthen with time since restoration,

although this process remains poorly documented in peatland pool systems. Despite growing interest in the role of restored pools in peatland recovery, most studies have focused either on vegetation colonization within pools after restoration (Fontaine et al., 2007; Mazerolle et al., 2006; Riaño Peña et al., 2026) or on large-scale spatial patterns in restoring former peat fields towards functioning peatland ecosystems (Breton et al., 2026; Nungesser, 2011; Poulin et al., 2013). Here, we examined how perpendicular environmental gradients associated with restored pools (created and spontaneous) in ombrotrophic peatlands influence vegetation specificity, and whether this spatial structuring strengthens with time since restoration relative to adjacent non-pool peatland areas. We sampled reference pools in undisturbed peatlands, as well as created and spontaneous pools in peatlands undergoing 6 to 26 years of restoration in eastern Canada (Quebec and New Brunswick). Based on this scheme, we addressed the following two research questions: (i) How does vegetation diversity and composition vary along the perpendicular gradient in restored pools compared with reference pools? (ii) Does the strength of this spatial structuring increase with time since restoration relative to adjacent non-pool peatland areas?

Materials and Methods

Study site

This study was conducted in 67 pools distributed across 9 reference peatlands and 12 peatlands restored using the Moss Layer Transfer Technique (MLTT; see González and Rochefort, 2014 for details), on former peatlands used for horticultural peat extraction. The pools were located in raised bogs across Eastern Canada (Figure 10), specifically within three climatic regions: Atlantic Canada (n reference [ref] = 6; n restored [res]= 8), the Great Lakes–St. Lawrence region (nref = 9; nres = 24), and the Northeastern Forest region (nref = 11; nres = 9) (Environment and Climate Change Canada, 2023). Together, these sites span a geographic gradient of approximately 500 km east–west and 600 km north–south. The raised bogs included in this study correspond to the maritime non-forested bogs with pool patterns that extend across the Gulf of St. Lawrence and the Maritime provinces of Canada (Glaser, 1992; Glaser and Janssen, 1986). Across Atlantic Canada, the Great Lakes region, and the Northeastern Forest, climatic conditions are broadly similar: all three climatic regions have cool temperate climates with mean annual temperatures ranging from 3.2°C to 4.8°C, annual precipitation close to 1,000–1,110 mm, and short growing seasons of 133 to 150 days. Although Atlantic Canada is shaped by a maritime climate, with cooler summers and milder winters, while the Great Lakes and Northeastern Forest regions experience more continental conditions, the overall climatic conditions remain broadly comparable, with all three regions exhibiting substantial seasonal variability (Environment and Climate Change Canada, 2023).

The reference peatlands were classified as ombrotrophic bogs according to the Canadian wetland classification system (National Wetlands Working Group, 1997). These peatlands were dominated by *Sphagnum* mosses and ericaceous shrub species (Zoltai and Vitt, 1995) and exhibited strongly acidic conditions, with a mean pH of 3.4 (SD = 0.4) and low electrical conductivity (49 µS/cm; SD = 16.1). Similarly, the restored peatlands remained ombrotrophic, with a mean residual peat thickness of 121 cm (SD = 62.3), an average pH of 3.7 (SD = 0.4), and an electrical conductivity of 111 µS/cm (SD = 101.4) (Andersen et al., 2011). All environmental data for the restored peatlands were obtained from the Peatland Ecology Research Group (PERG) long-term monitoring program.

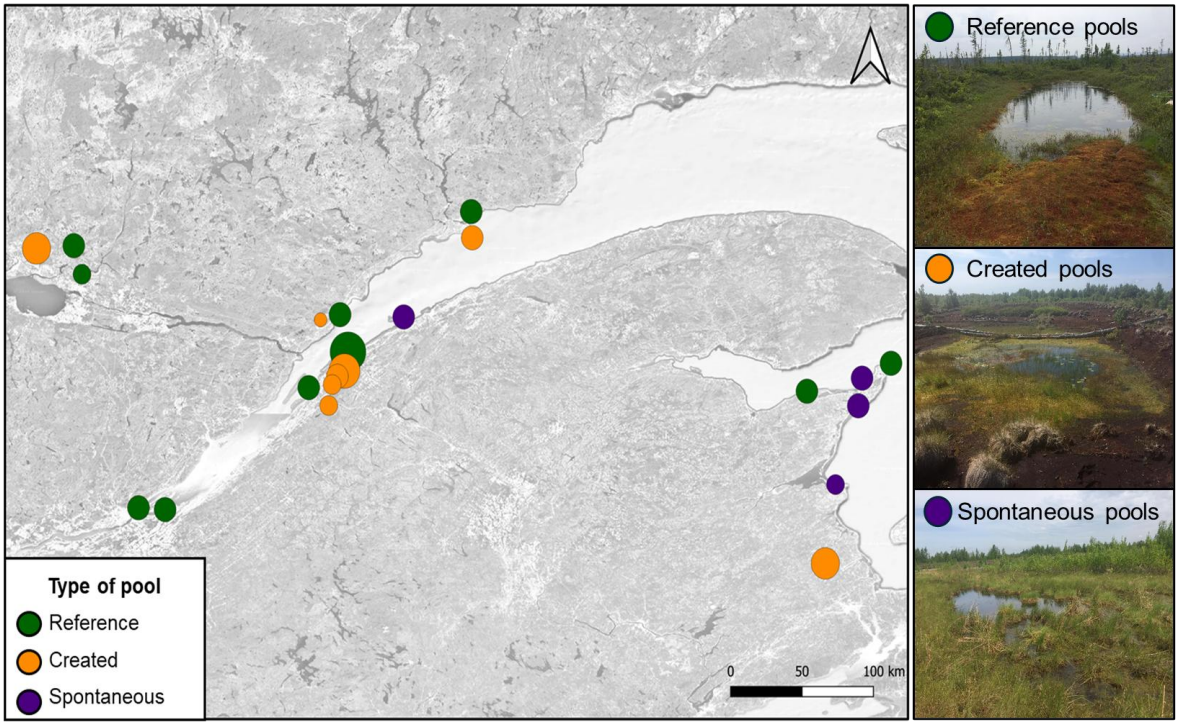

Figure 10. Location of the 67 surveyed pools on 21 peatlands (9 reference peatlands and 12 restored peatlands) in the provinces of Quebec and New Brunswick (Eastern Canada), accompanied by pool types [reference (n = 26), created (n = 19), and spontaneous (n = 22)]. Points' size increases with the number of associated pools. This map was created using ArcGIS Desktop 10.8.2, sourced from OpenStreetMap contributors. Map projection: Lambert Conformal Conic (NAD83(CSRS)/Canada Lambert, EPSG:3978). Credit for the photos: Laura Catalina Riaño Peña.

Pool selection

The surface of each peatland was examined using Google Earth satellite imagery to visually identify existing pools. Reference pools were chosen to capture a broad range of shapes and sizes by including large, medium, and small pools (perimeter ranged from 25 to 340 m). At each site, between 2 and 6 pools were selected to represent the local variability in pool surface area, and their depths were later measured directly in the field. In total, 26 reference pools and 41 pools within restored peatlands were identified and surveyed (Appendix 3.1). In restored sites, we classified two types of microforms as pools: those intentionally constructed as part of ecological restoration efforts (n = 19) and those that formed naturally, either in wetter zones of the residual topography or following the passage of heavy machinery (n = 22). To be included in the study, pools in restored peatlands had to meet two additional conditions: they had to be located in restored bogs, and selected sites (not the pools) had to show clear signs of successful vegetation recovery, defined by an average plant cover of at least 40%, dominated by Sphagnum and other moss species (González et al., 2014). None of the restored pools received active revegetation treatments, neither through seeding nor transplants of species typical of bog pools. Based on time since restoration, sites were then classified into two age groups: a "young" group, consisting of bogs restored in or after 2008 (6–13 years since restoration), and an "old" group, consisting of bogs restored before 2008 (15–26 years since restoration). Consequently, plant colonization in these pools likely reflected a combination of inputs from the MLTT and natural colonization processes, shaped by local context such as the proximity of other restored areas, nearby natural peatlands, and human-modified environments such as agricultural or grazing lands.

Vegetation survey

Pools were sampled during the summer of 2021 (June to August) using four transects laid out perpendicular to the pool edge (perpendicular gradient). For natural pools (n = 26) and created pools (n = 19), two transects were placed on gentler slopes and two on steeper slopes to capture the variation in surrounding topography. Spontaneous pools, which generally occur in areas with little topographic variation, were also sampled with four transects, although these usually represented similar slope conditions (n = 22; Figure 10). Along each transect, four circular quadrats with a diameter of one meter were sampled. The first quadrat was placed directly in the water at the pool margin, the second just outside the standing water at the edge, the third at 2 meters from the edge, and the fourth at 10 m from the pool's edge, well beyond the pool perimeter. In each plot (n = 1072), we estimated the cover of the following vegetation strata: ericaceous shrubs, other shrubs, herbaceous species, and mosses (including *Sphagnum*, liverworts, and other moss taxa). Species were identified to the finest taxonomic level possible, and cover estimates reflected their vertical projection onto the ground. Unknown

species were collected in the field and later identified in the laboratory. Taxonomic nomenclature followed *Flore des bryophytes du Québec-Labrador* (Faubert, 2012) for bryophytes, *Sphagnum Mosses of Eastern Canada* (Ayotte and Rochefort, 2020) for *Sphagnum*, and *Flora of North America* (Morin, 2000), as well as VASCAN, the Database of Vascular Plants of Canada (Brouillet et al., 2021), for vascular plants.

Vegetation classification

To assess how environmental gradients influence perpendicular connectivity in terms of vegetation composition across different pool types, we categorized all recorded plant species, including both bryophytes and vascular plants, into functional groups based on their ecological traits. Drawing on a comprehensive review of the literature (Faubert, 2012; Lachance et al., 2021; Lemmer et al., 2023; Morin, 2000; Payette and Rochefort, 2001; Vitt, 2014), each species was assigned to one of three mutually exclusive habitat-based categories. The decision-making process used to define these categories followed the same approach as that described by Riaño Peña et al. (2026) for species associated with ombrotrophic peatland pools:

1. Species preferring open-water pools of *Sphagnum*-dominated peatlands (POOL): this category comprises ombrotrophic peatland species that are occasionally, frequently, or preferentially present on the edges of or within pools of undisturbed *Sphagnum*-dominated peatlands.

2. Species preferring *Sphagnum*-dominated peatlands microforms, other than pools (BOG): This category includes ombrotrophic peatland species found in microforms other than pools within peatlands, such as hummocks, spruce thickets, and laggs, and that are rare or absent from the pools or the edges of pools of undisturbed reference *Sphagnum*-dominated peatlands.

3. Species preferring other habitats than *Sphagnum*-dominated peatlands (OTHER): This category includes all species absent or rare in *Sphagnum*-dominated peatlands, with species commonly found in lawn habitats, alongside species typically found in various types of wetlands.

Environmental conditions

Environmental conditions at each pool were described using several parameters. The coordinates of each pool (i.e., latitude and longitude) were recorded with a GPS tablet using an offline mapping application, Avenza Maps (5 – 10 meters of spatial precision). The perimeter of the pools was assessed using satellite imagery sourced from Google Earth in winter 2021. The presence of ice on the pool surfaces has enabled a more precise assessment of their extent using satellite imagery. The depth of the pools was measured using a 4m string attached to a disk, ensuring minimal disruption to the pool bed, which comprised unconsolidated sediments. To characterize the chemical properties of the pools, in-water measurements were taken, pH was directly assessed in the field (one measurement per pool) using a pH meter (HI98129, Hanna Instruments).

Statistical analysis

All statistical analyses were performed using RStudio (R Core Team 2022, version 4.2.2) software. Before the analyses, the environmental datasets were cleaned and harmonized at the pool level. Pool type was treated as a three-level factor (reference, created, and spontaneous), and plot distance was treated as a four-level factor (0, 1, 2, and 10 meters). Restored peatlands were divided into two categories based on post-restoration age: old peatlands (restored before 2008) and younger peatlands (restored in or after 2008). Old peatlands included 24 restored pools (11 created and 13 spontaneous), corresponding to 15–26 years since restoration at the time of the 2021 survey.

Variations in the richness of total plant species (TOTAL), the richness of species preferring pools (POOL), and the richness of species preferring other *Sphagnum*-dominated peatland microforms (BOG) were tested using Generalized linear mixed-effects models (GLMMs, Bolker et al., 2009) with a negative binomial error distribution. Analyses were conducted separately for young and old restored peatland pools, and the variable distance, pool type, and their interaction were used as fixed effects. Site was included as a random intercept to account for non-independence of observations within peatlands. Model assumptions were evaluated using scaled residuals (Harting and Harting, 2017). Marginal and conditional R^2 values were calculated to assess model fit. For graphical representation and post hoc interpretation, distance was treated as a categorical factor, and estimated marginal means were computed on the response scale with 95% confidence intervals.

Finally, differences in species composition were assessed using permutational multivariate analyses of variance (PERMANOVA; vegan R package, Oksanen et al., 2024) with pool type, distance, and their interaction as fixed effects. Multivariate analyses were performed on Bray–Curtis dissimilarity matrices, after excluding species present in fewer than three plots. Analyses were conducted separately for young and old restored pools, rather than comparing these age groups directly. The site name was used as a stratification factor to account for spatial structure among peatlands. Pairwise PERMANOVA (Martinez Arbizu, 2020) comparisons among pool type-distance combinations were conducted with false discovery rate correction. Homogeneity of multivariate dispersion within each factor level was assessed using PERMDISP (vegan R package, Oksanen et al., 2024) based on distances to group centroids. Significance was evaluated with permutation tests (999 permutations) (Anderson and Walsh, 2013). Patterns in species composition were visualized using principal coordinates analysis (PCoA), with ellipses representing group dispersion and centroids displayed for each pool type-distance combination. In addition, for both young and old peatland restored pools, Pearson's *phi* coefficient of association (indicspecies R-package, Caceres and Legendre 2009), corrected for unequal group sizes, was used to identify species significantly associated with specific pool type-distance combinations, using permutation tests (n = 999).

Results

Variations in species richness along the perpendicular gradient across pool types in young and old restored peatlands

When comparing plant communities in young, restored peatlands to reference sites, we found that TOTAL species richness increased significantly along the perpendicular gradient, but the effect differed among pool types in young, restored peatlands (i.e., significant interaction effect, Table 6). In spontaneous pools, the increase was gradual across the entire gradient, whereas in created and reference pools, it was restricted to the first two quadrats (0 and 1 m). In contrast, in old, restored peatlands, TOTAL species richness increased similarly across the perpendicular gradient for all three pool types. In addition, TOTAL species richness was significantly higher for reference pools than for spontaneous and created pools. However, the magnitude of this effect decreased with time since restoration, particularly for created pools (Figure 11, Table 6).

BOG species richness increased similarly along the perpendicular gradient regardless of pool type in both young and old peatlands (Table 6, Figure 11). Nevertheless, reference pools consistently supported higher BOG species richness than spontaneous and created pools, regardless of peatland age, although this difference tended to diminish with time since restoration, most notably for created pools in old, restored peatlands.

POOL species richness decreased along the perpendicular gradient for the three types of pools, but the slope of this decline varied among pool types in both young and old peatlands. Furthermore, reference pools had overall higher POOL species richness than spontaneous and created pools at short distances (0 and 1 m), but this difference decreased along the perpendicular gradient and eventually disappeared at greater distances. This pattern is supported by negative main effects of pool type (S and Cr) and positive interactions with distance, indicating convergence in species richness with increasing distance (Figure 11, Table 6).

Table 6. Results from a negative binomial generalized linear mixed model (GLMM) testing the effects of distance to pools (Dist), pool type (spontaneous = S, created = Cr), and their interaction on TOTAL, BOG and POOL plant species richness in young and old restored peatlands. Site was included as a random intercept in *Sphagnum*-dominated peatlands in Eastern Canada (Quebec and New Brunswick). Significance levels are indicated by asterisks (* p < 0.05, ** p < 0.01, *** p < 0.001).

PREDICTOR	TOTAL (young)	TOTAL (old)	BOG (young)	BOG (old)	POOL (young)	POOL (old)
Intercept	2.22***	2.22**	1.64***	1.64***	1.35***	1.36***
Dist	0.031***	0.031***	0.076***	0.075***	-0.113***	-0.113***
Type pool (S)	-0.585***	-0.495***	-0.764***	0.529***	-0.974***	-0.614***
Type pool (Cr)	-0.505***	-0,247**	-0.776***	-0.235*	-0.675***	-0.422***
Dist x S	0.029**	0.017	0.020	0.009	0.074***	0.098***
Dist x Cr	-0.004	0.015	-0.012	0.005	0.085***	0.054**

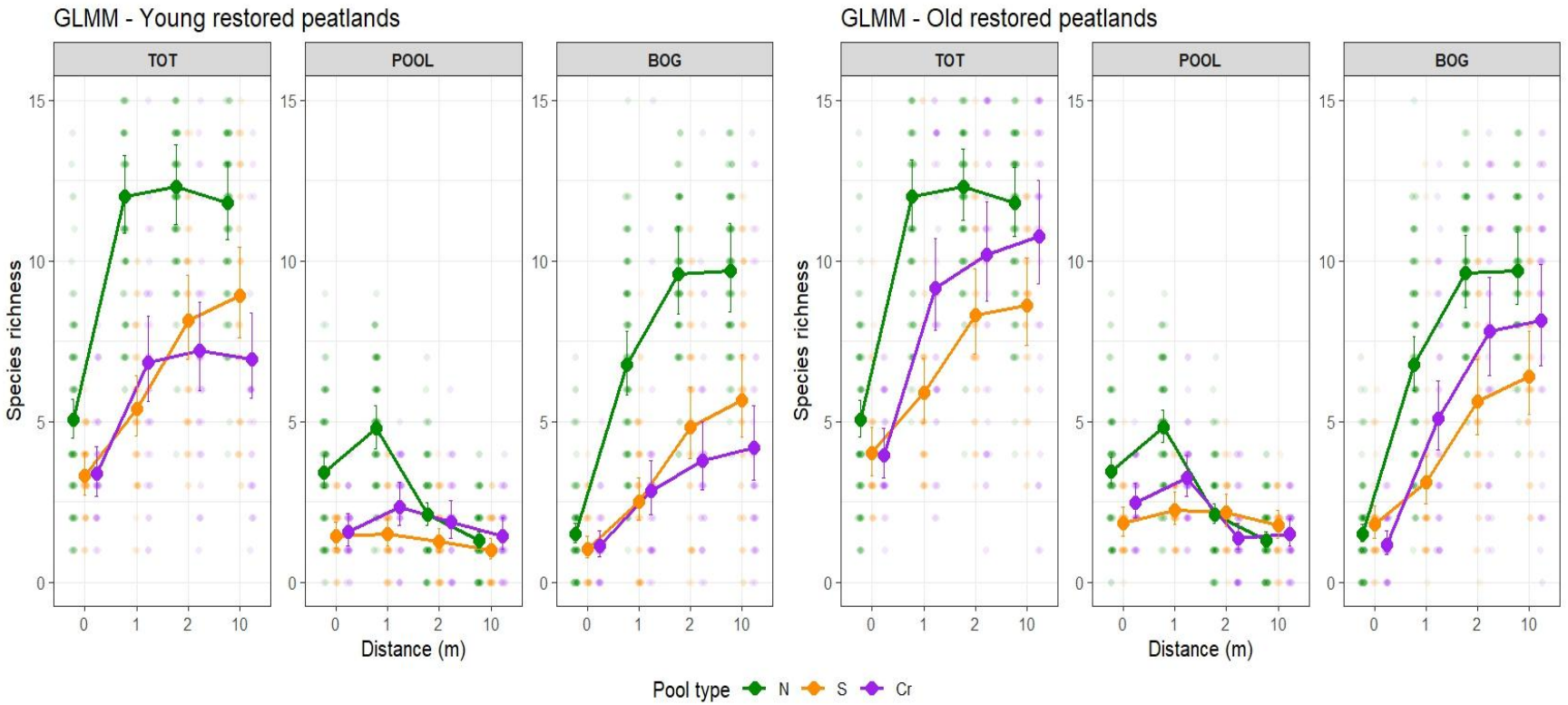

Figure 11. Species richness of the three categories of species classification [TOTAL (all species combined), BOG (species typical of other bog microforms) and POOL (typical pool species). Divided into young restored peatland pools (6 – 13 years since restoration) and old restored peatland pools (11 – 26 years since restoration), making a distinction between the plant species composition and the four distances of plots (0, 1, 2 and 10 meters), in the three types of pools in *Sphagnum*-dominated peatlands in Eastern Canada (Quebec and New Brunswick).

Variations in species composition along the perpendicular gradient across pool types in young and old restored peatlands

Species composition differed significantly along the perpendicular gradient, with differences among pool types observed in both young and old peatlands (Figure 12). This turnover was slightly stronger in young than in old peatlands (PERMANOVA for the interaction between pool type and distance: Young: $F = 19.68$, $R^2 = 0.118$, $p = 0.001$; Old: $F = 17.45$, $R^2 = 0.107$, $p = 0.001$). Graphical interpretation suggests that species composition changed markedly over a short distance in reference pools along the perpendicular gradient, with a pronounced shift between quadrats 0 and 1, followed by a smaller change between quadrats 1 and 2, and little differentiation thereafter. In contrast, restored pools showed a more gradual change in composition along the gradient. In contrast, restored pools showed limited compositional change along the gradient in young peatlands, but a more pronounced turnover with increasing distance in old peatlands, indicating a more structuring effect of the perpendicular gradient over time. This pattern is supported by pairwise comparisons, which revealed significant effects of distance within pool types (for more details, see Figure 13). In addition, the degree of plot dispersion around the centroids of each group, i.e., pool type, was significant both for young (PERMDISP, $F = 15.11$, $p = 0.001$) and old peatlands ($F = 7.82$, $p = 0.001$). This indicates variation in community composition across the perpendicular gradient as well as differences in within-pool variability. The spatial organization of community composition along the gradient was present in both age classes but was more pronounced in old peatlands. The main gradient identified (11.9–14.4% of the explained variance) reflects this spatial variation in community composition along the gradient (Figure 12).

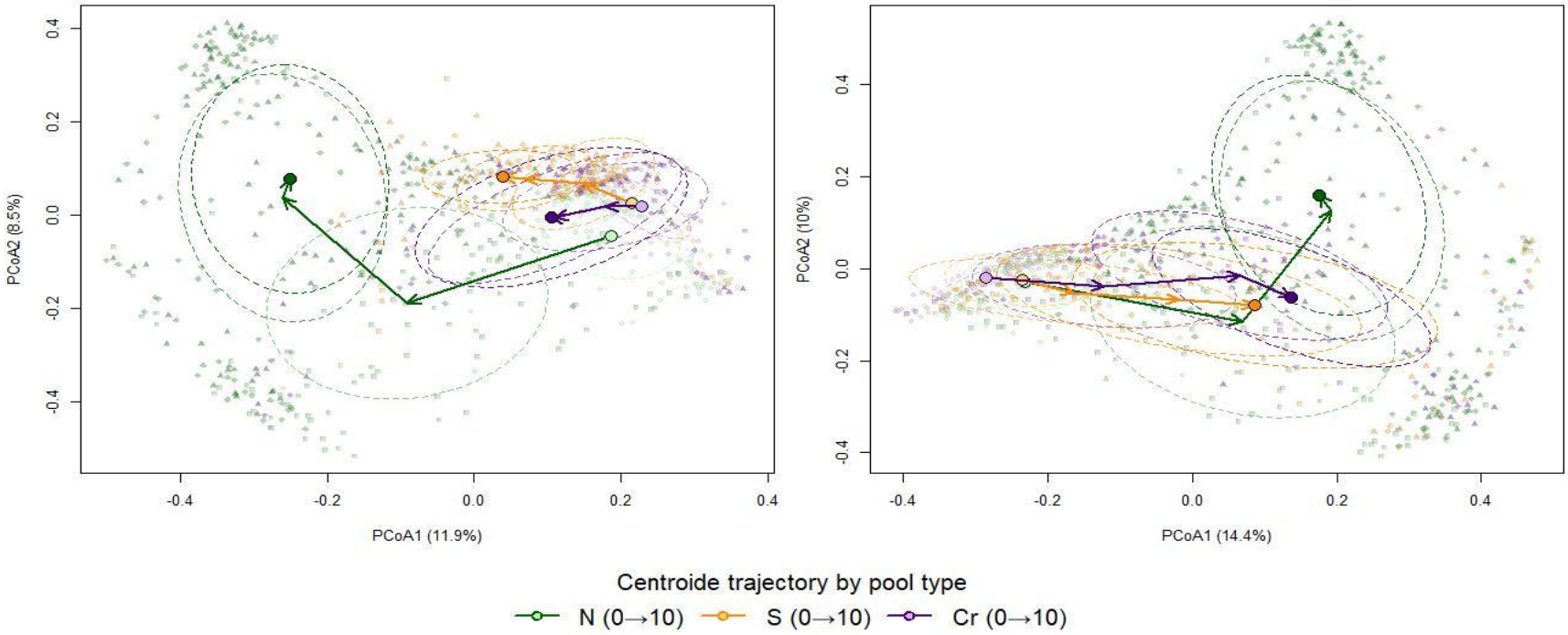

Figure 12. Plant community composition in restored peatland pools as revealed by Principal Coordinates Analysis (PCoA). The ordination is based on Jaccard dissimilarities calculated from species presence–absence data. Each point represents a sampling plot (vegetation relevé), not an individual species, and reflects the plant community composition at a given distance from the pool edge (0, 1, 2, and 10 m). Panels distinguish young restored pools at the left (6–13 years since restoration) and old restored pools at the right (11–26 years since restoration), and comparisons are shown among the three pool types (N = natural, S = spontaneous, Cr = created) in Sphagnum-dominated peatlands of Eastern Canada (Quebec and New Brunswick, Appendix 3.1). Centroids (colored dots) represent mean community composition for each pool type at each distance, and trajectories illustrate compositional shifts along the distance gradient. Ellipses represent 95% confidence intervals around group centroids.

Reference pools showed the clearest pattern of species-habitat association, with 21 species significantly associated with reference pools (see phi coefficient of association, Table 7). Specifically, in reference pools, three species were associated with distance 0 (open water of the pool) (*Carex limosa*, *Nuphar advena*, *Rhynchospora alba*), six with distance 1 (at 1 meter to the edge of the pool) (including *Andromeda polifolia*, *Sphagnum medium*, *S. rubellum*), five with distance 2 (at 2 meters to the distance 1) (e.g., *Sphagnum fuscum*, *Rubus chamaemorus*, *Vaccinium oxycoccos*), and seven with distance 10 (at 10 meters to the distance 2) (e.g., *Kalmia angustifolia*, *Dicranum undulatum*, *Gaylussacia baccata*). For created pools located in young peatlands, three associated species were identified: one at distance 0 (open water of the pool) (*Juncus tweedyi*) and two at 1 meter from the edge of the pool (*Carex canescens, Hypericum fraseri*). For old peatlands created pools, only one species was identified, i.e., *Typha latifolia,* linked to the open water of the pool. For spontaneous pools in young peatlands, five species were highlighted, including two in the open water of the pool (*Sphagnum fallax, Typha latifolia*), one at 1 meter to the edge of the pool (*Eriophorum vaginatum*), and two at 10 meters to distance 2 (*Betula papyrifera, Polytrichum strictum*). For spontaneous pools in old peatlands, five species were identified: two species linked to open water of the pool (*Carex oligosperma, Warnstorfia fluitans*), two species at 1 meter from the edge of the pool (*Carex canescens, Sphagnum fallax*), and one species at 2 meters from distance 1 (*Chamaedaphne calyculata*).

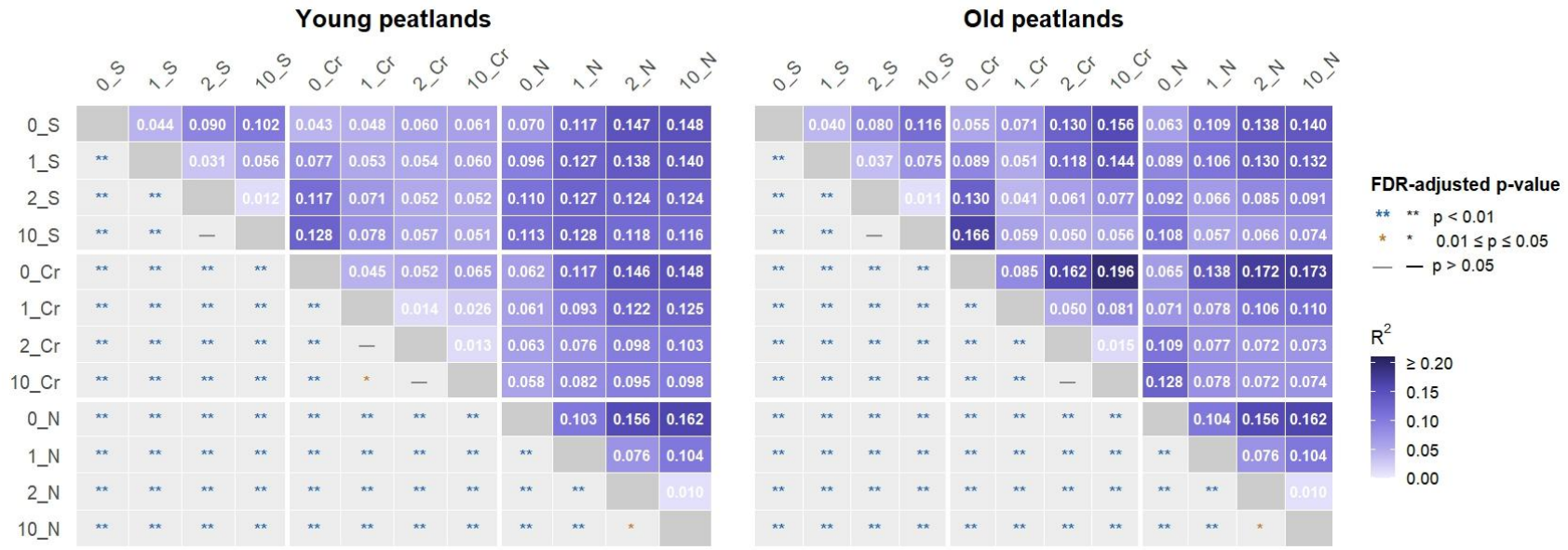

Figure 13. Pairwise comparisons between the types of pools (reference = N, created = C and spontaneous = S), for young restored peatland pools (6 – 15 years since restoration) and old pools (15 – 26 years since restoration), making a distinction between the plant species composition and the four distances of plots (0, 1, 2 and 10 meters), in *Sphagnum*-dominated peatlands in Eastern Canada (Quebec and New Brunswick).

Table 7. List of plant species significantly associated with the three types of pools (reference, created and spontaneous). Divided into young restored peatland pools (6 – 13 years since restoration) and old restored peatland pools (15 – 26 years since restoration) in *Sphagnum*-dominated peatlands in Eastern Canada (Quebec and New Brunswick).

	Distance	Species	Stat
Reference pools	0	*Carex limosa*	0,3827
	0	*Nuphar advena*	0,4137
	0	*Rhynchospora alba*	0,2737
	1	*Andromeda polifolia*	0,3389
	1	*Drosera rotundifolia*	0,2283
	1	*Eriophorum virginicum*	0,2646
	1	*Sarracenia purpurea*	0,2229
	1	*Sphagnum medium*	0,3995
	1	*Sphagnum rubellum*	0,2763
	2	*Kalmia polifolia*	0,2932
	2	*Mylia anomala*	0,2725
	2	*Rubus chamaemorus*	0,3321
	2	*Sphagnum fuscum*	0,3554
	2	*Vaccinium oxycoccos*	0,2985
	10	*Chamaedaphne calyculata*	0,2332
	10	*Dicranum undulatum*	0,3050
	10	*Gaylussacia baccata*	0,3029
	10	*Kalmia angustifolia*	0,4215
	10	*Picea mariana*	0,2912
	10	*Rhododendron groenlandicum*	0,2460
	10	*Vaccinium angustifolium*	0,2609
Created pools/young	0	*Juncus tweedyi*	0,3908
	1	*Carex canescens*	0,3800
	1	*Hypericum fraseri*	0,3237
Created pools/old	0	*Typha latifolia*	0,5825
Spontaneous pools/young	0	*Sphagnum fallax*	0,2810
	0	*Typha latifolia*	0,2262
	1	*Eriophorum vaginatum*	0,3211
	10	*Betula papyrifera*	0,1908
	10	*Polytrichum strictum*	0,2874
Spontaneous pools/old	0	*Carex oligosperma*	0,3052
	0	*Warnstorfia fluitans*	0,2464
	1	*Carex canescens*	0,2802
	1	*Sphagnum fallax*	0,2694
	2	*Chamaedaphne calyculata*	0,2602

Discussion

This study investigates variations in species diversity and composition in open-water habitats within restored, *Sphagnum*-dominated peatlands, focusing on created and spontaneous pools distributed across Eastern Canada. By comparing created and spontaneous pools post-restoration to natural reference pools, we reveal significant differences in community structure. Specifically, vegetation showed strong variation along the perpendicular hydrological gradient across all three pool types, indicating that this gradient promotes the formation of distinct species assemblages and contributes to increasing the overall species pool of *Sphagnum*-dominated peatlands. Furthermore, we highlighted that species richness in both spontaneous and created pools tended to converge toward reference conditions over time. This pattern was most evident in created pools within older peatlands, where richness became similar to that of the reference. However, species composition did not follow the same trajectory. Clear differences persisted, particularly at 2 meters and 10 meters, where reference pools supported distinct assemblages compared to both created and spontaneous pools. At these distances, spontaneous pools generally exhibited a composition closer to the reference condition in terms of target species, whereas created pools remained more distinct. Overall, these results indicate a partial convergence toward reference conditions, driven primarily by changes in species richness rather than community composition.

Variation in diversity and composition along perpendicular gradients

Vegetation diversity and composition in peatland pools were strongly structured by distance from the pool, indicating a clear spatial gradient from the aquatic environment toward the surrounding peatland vegetation (Noleto et al., 2019; da Silveira et al., 2025). This distance-based pattern is consistent with well-established ecological gradients in wetland systems, where changes in hydrological conditions, substrate characteristics, and associated physicochemical properties typically occur over short spatial scales and influence plant community assembly (Keddy, 2010; Rydin and Jeglum, 2013; Noleto et al., 2019). Within this context, plots located at 0–1 m were dominated by aquatic and semi-aquatic species (e.g., *Nuphar advena*, *Carex limosa*), whereas plots located at 2–10 m were characterized by ericaceous shrubs and woody taxa (e.g., *Kalmia polifolia*, *Picea mariana*). This pattern is well illustrated for reference pools, which show a classic peatland zonation driven by species-specific tolerances to flooding and desiccation in water bodies (Molina and Navarro, 2025; Wheeler and Proctor, 2000; Whitehouse and Bayley, 2005). Intermediate distances (2 m) hosted transitional plant communities, founded in both wetter and drier environments (e.g., *Mylia anomala*), suggesting that many peatland species exhibit relatively broad ecological amplitudes (Benavides and Vitt, 2014; Gignac et al., 1991; Gignac, 1994). Such overlap is typical of hydrologically dynamic systems, where fluctuating water levels favour species capable of tolerating variable conditions of inundation (Merrit et al., 2010; Roznere and Titus, 2017). As a result, vegetation patterns along the perpendicular gradient can be understood as a continuum rather than discrete zones.

Species richness showed contrasting patterns depending on species categories along the perpendicular gradient. The richness of BOG and TOTAL species increased with distance from the pool, reaching higher values in areas further away. In contrast, POOL species richness decreased with increasing distance, with higher values recorded close to the pool edge. Created pools initially had lower richness in the three categories (TOTAL, BOG, POOL) than reference pools but tended to converge over time towards comparable levels of species richness. Despite this, compositional differences remain; created pools were often dominated by generalist species (e.g., *Typha latifolia*), whereas spontaneous pools maintained more complex and characteristic assemblages of *Sphagnum*-dominated peatlands (e.g., *Carex oligosperma* and *Warnstorfia fluitans*). These differences can be influenced by hydrology and the morphology of the pools. Created pools typically have steep edges, which act as abiotic filters, limiting the contact with the water and favouring early colonizers (Butterfield and Palmquist, 2024; Pellerin et al., 2009). Water level fluctuations are generally accepted as an environmental factor that determines the growth and survival of different species and can influence the structure of plant communities in wetlands (Wassen et al., 2003; Luo et al., 2008; Keddy, 2010). In contrast, spontaneous pools form in gentler depressions offering gradual transitions from open water to peat, allowing a wider range of species, including peat-forming specialists (e.g., *Sphagnum fallax*). The presence of a gentle slope promotes more natural successional trajectories in plant colonization (Liu et al., 2014). Early attempts to create pools in restored peatlands (Quinty and Rochefort, 2003) assumed greater water-level fluctuations (McCarter and Price, 2015; Price, 1996), leading to the design of deeper pools to ensure permanent water. However, spontaneous pools better reflect natural peatland dynamics, as their formation and morphology respond to hydrological and climatic conditions (Karofeld, 1998; Walker and Walker, 1961). Periods of higher moisture promote hollow expansion, while drier conditions lead to contraction, helping regulate water balance (Karofeld and Tõnisson, 2014). Hollow development is also directionally constrained: expansion occurs mainly along their longitudinal axis, as upslope and downslope growth are limited by environmental factors. Consequently, hollows are typically oriented perpendicular to the slope and surface flow, further emphasizing the role of hydrology and microtopography in shaping natural pool development (Karofeld and Toom, 1999; Karofeld et al., 2008).

Strengthening of spatial structuring with time since restoration

The strength of spatial structuring increased with time since restoration, although this pattern varied among pool types. In older peatlands, vegetation composition showed greater differentiation along the perpendicular gradient, particularly in created pools, where species turnover between distances near the pool (0 and 1 m) and more distant plots (2 and 10 m) becomes more pronounced. This indicates that the structure of plant communities, as restored peatlands mature, is consistent with increasing habitat stability and peat accumulation over time (Alderson et al., 2019; Breton et al., 2026; Haapalehto et al., 2017).

Temporal changes can influence species richness and composition. In created pools, richness generally increased with time since restoration, and pools located in older peatlands can approach reference pools in terms of species numbers. However, compositional convergence remained limited, with created pools often dominated by a subset of competitive generalist species, even decades after restoration (e.g., *Hypericum fraseri*, *Typha latifolia*). Created pools in young peatlands were initially characterized by early colonizers such as *Juncus* spp., which likely established on newly exposed, bare substrates following disturbance. This pattern is consistent with colonization of thin peat layers where roots can access the underlying mineral substrate, facilitating early establishment (McCorry and Renou, 2003; Richards and Clapham, 1941). Its early dominance suggests strong colonization of open surfaces rather than transitional wet conditions, and it may be progressively replaced over time through competitive interactions with other plant species (Keightley et al., 2025). Over time, these pools tended toward simplified communities dominated by a few competitive species, suggesting that richness recovery does not necessarily translate into full compositional recovery. This pattern is consistent with biotic homogenization processes, whereby communities become increasingly similar over time due to the dominance of widespread generalist species and the loss or limited establishment of specialistic taxa (Filgueiras et al., 2021; Olden et al., 2004). Spontaneous pools, in contrast, supported higher compositional complexity across both young and old peatlands, supporting species like *Carex* spp, *Warnstorfia fluitans* and *Sphagnum fallax*, which showed clearer progression toward typical peatland assemblages, indicating a trajectory more consistent with natural pool development. Although community responses to the perpendicular gradient become more similar among pool types with age, full convergence toward reference conditions remained incomplete. Adjacent non-pool peatland areas, less constrained hydrologically, showed stronger increases in richness with time, suggesting that these areas may recover more rapidly than areas directly influenced by the pool. This pattern can reflect differences in colonization dynamics; aquatic and semi-aquatic pool species often depend on more specialized or stochastic dispersal pathways and stricter establishment conditions (Santamaria, 2002; Soons, 2006), whereas peatland species can disperse and establish more easily via the MLTT method (Hugron et al., 2020; Rochefort et al., 2003). As a result, adjacent areas may accumulate species more rapidly than pool microforms.

Implications for restoration

From a restoration perspective, these findings suggest that perpendicular gradients can gradually be re-established over time, representing an important step toward microform recovery. The development of spatial heterogeneity is particularly relevant, as it supports diverse species assemblages and enhances overall ecosystem diversity (Caners et al., 2019; Erdős et al., 2018; Wojciechowski et al., 2024). However, the incomplete convergence in species composition highlights persistent limitations in restored pools.

Management actions could therefore focus on improving the establishment of target species, either by increasing propagule availability through active introduction of pool specialists or by facilitating natural dispersal processes. In addition, modifying microtopographic conditions to reduce the steepness of the gradient may help accelerate convergence toward reference pool communities. Prioritizing conditions that promote gradual transitions from open water to peat may further support the colonization of peatland pool specialists and enhance successional development.

Appendices

Table 3. 1. List of peatlands where pools were sampled, divided between the three types of climatic regions, in *Sphagnum*-dominated peatlands pools [reference (*n* = 26), created (*n* = 19), spontaneous (*n* = 22)], in Eastern Canada (Quebec and New Brunswick).

			Type of pool		
Region	**Site and sector**	**Sector location**	**Created**	**Spontanous**	**Natural**
Atlantic Canada	Pokesudie M2006	47.819770,-64.780825	3	0	0
	Inkerman Ferry R2008	47.705859,-64.818340	3	0	0
	Baie-Sainte-Anne M2015	46.987330,-64.999917	2	0	0
	Miscou	47.9384280,-64.5226109	0	0	3
	Black-rock	47.7149709,-65.2725914	0	0	3
Great Lakes and St Lawrence	Chemin du Lac R1995	47.768372,-69.526130	0	2	0
	Saint-Modeste R2013	47.833743,-69.462967	0	3	0
	Président-Ouest R2012	47.786055,-69.491455	0	2	0
	Verbois R2006	47.836220,-69.440585	0	6	0
	Bois-des-Bel R1995	47.967220,-69.430198	8	0	0
	Saint-Fabien-sur-Mer R2011A	48.308628,-68.870688	3	0	0
	Saint-Alexandre-du-Kamouraska	47.739855,-69.610953	0	0	3
	Saint-Charles-de-Bellechase	46.769227,-71.000235	0	0	3
	Grande-Plée-Bleue	46.779833,-71.056853	0	0	3
Northeastern Forest	Sainte-Marguerite-Marie AA2001	48.827642,-72.175940	0	5	0
	Ascension	48.757045,-71.728222	0	0	2
	Saint-Ludger	48.877983,-71.815078	0	0	3
	Pointe-Lebel RA2010	49.156588,-68.259053	0	3	0
	Escoumins R2011	48.317282,-69.434713	0	1	0

	Pointe-Lebel	49.150505,-68.268145	0	0	3
	Escoumins	48.3270394,-69.4388613	0	0	3

Table 3. 2. Variations in spatial and morphological conditions (mean ± standard deviation) between the three types of pools in *Sphagnum*-dominated peatlands in Eastern Canada (Quebec and New Brunswick). Restored pools (created and spontaneous) were divided into two groups: young restored peatlands (6-15 years since restoration) and old restored peatlands (15 – 26 years since restoration) in *Sphagnum*-dominated peatlands in Eastern Canada (Quebec and New Brunswick).

		Young restored peatlands		Old restored peatlands			
Variable	**Reference pools**	**Spontaneous pools**	**Created pools**	**Spontaneous pools**	**Created pools**	**X-value**	**p-value**
Latitude (Lat; ◦)	69.09 (±2.59)	69.16 (±0.54)	66.16 (±2.04)	70.83 (±1.43)	68.54 (±1.87)	25.89	**0.000**
Longitude (Long; ◦)	47.98 (±0.83)	48.2 (±0.6)	47.94 (±0.28)	48.31 (±0.53)	47.77 (±0.41)	3.44	0.486
Perimeter (Perimeter; m)	95 (±90.3)	38 (±32.3)	45 (±18.89)	52 (±101.71)	45 (±6.99)	20.27	**0.000**
pH	3.41 (±0.46)	3.86 (±0.92)	3.7 (±0.68)	3.65 (±0.62)	4 (±0.52)	7.16	0.127
Depth (Depth; cm)	106 (±66.96)	32 (±16.9)	73 (±50.07)	20 (±7.38)	44 (±23.71)	35.80	**0.000**

Conclusion

Généralités

La restauration des tourbières constitue une opportunité de recréer des microformes essentielles à la biodiversité, notamment les mares, qui contribuent à l'hétérogénéité structurelle et à la diversité des communautés végétales au sein des tourbières qui les abritent. Cependant, les activités anthropiques ont profondément modifié ces écosystèmes, rendant nécessaire le développement de stratégies de restauration capables de rétablir à la fois des conditions abiotiques et les communautés végétales caractéristiques.

Dans cette thèse, je me suis intéressée à la diversité végétale associée aux mares dans les tourbières restaurées et naturelles, afin d'évaluer dans quelle mesure les pratiques actuelles de restauration permettent de recréer ces habitats et de favoriser le retour des communautés végétales spécialisées. Plus spécifiquement, cette recherche visait à mieux comprendre comment les conditions environnementales, les choix de conception et le contexte régional influencent le rétablissement de la végétation des mares.

La question centrale de cette thèse peut être formulée ainsi : comment favoriser le rétablissement de communautés végétales caractéristiques des mares dans les tourbières restaurées, en tenant compte des contraintes environnementales et des pratiques de restauration ? Pour y répondre, trois objectifs spécifiques ont été abordés :

1. Déterminer les variables environnementales influençant l'établissement de la végétation dans différents types de mares en tourbières ombrotrophes.

2. Identifier les communautés végétales associées aux mares en contexte minérotrophe et évaluer l'influence des facteurs environnementaux et du contexte régional.

3. Évaluer l'effet des gradients perpendiculaires autour des mares restaurées sur la spécificité de la végétation.

Deux grands constats émergent de cette thèse. Premièrement, bien que les pratiques de restauration permettent de recréer certaines conditions favorables, elles ne suffisent pas toujours à rétablir pleinement la diversité et la composition des communautés végétales caractéristiques des mares de référence. Deuxièmement, la prise en compte conjointe des facteurs environnementaux (chimie de l'eau, hydrologie) et des caractéristiques physiques (morphologie, gradients) est essentielle pour améliorer l'efficacité des interventions de restauration. Ces

résultats confirment l'hypothèse centrale de cette thèse, selon laquelle les mares présentes dans les tourbières restaurées présentent une diversité et une composition végétale différentes de celles des mares de référence, en raison des différences dans les conditions environnementales et des choix de conception et d'aménagement qui ne reproduisent pas entièrement les conditions des mares de référence.

Contributions principales

Comprendre les facteurs limitant la restauration de la végétation des mares en tourbières ombrotrophes

Les mares des tourbières jouent un rôle important dans le maintien de la biodiversité, en abritant des communautés végétales spécialisées adaptées à des conditions hydrologiques et chimiques particulières (Beadle et al., 2015; Arsenault et al., 2019; Jolin et al., 2024). En contexte de restauration, la création de ces habitats repose souvent sur des interventions physiques, comme le creusement de mares (Quinty et Rochefort, 2003), en supposant que les communautés végétales se rétabliront avec le temps sans réintroduction active. Toutefois, les facteurs qui limitent ou favorisent cet établissement demeurent encore mal compris, en particulier ce qui concerne l'interaction entre conditions environnementales et caractéristiques physiques des mares.

Les résultats du Chapitre 1 montrent que les mares restaurées présentent des conditions physico-chimiques distinctes, notamment des concentrations plus élevées en nutriments, ce qui favorise les plantes vasculaires au détriment des mousses typiques comme les sphaignes. La morphologie des mares restaurées agit également comme un filtre écologique influençant l'établissement des espèces. Bien que la technique de création des mares de Quinty et Rochefort (2003) permette de recréer un couvert végétal comparable en termes de recouvrement total à celui des mares de référence, elle ne permet pas de retrouver une richesse spécifique équivalente et s'accompagne d'une plus grande variabilité dans la composition des communautés, souvent dominée par des espèces non ciblées par les objectifs de restauration des mares.

Ces résultats mettent en évidence que la simple création de mares ne suffit pas à recréer des conditions écologiques équivalentes à celles des mares de référence. Ils soulignent la nécessité d'intégrer à la fois la conception des mares et le contrôle des conditions environnementales pour améliorer les résultats de restauration. Dans cette perspective, il devient essentiel de mieux comprendre comment ces facteurs varient selon les contextes écologiques, notamment dans les tourbières minérotrophes, où les contraintes environnementales diffèrent de celles des tourbières ombrotrophes, en particulier en ce qui concerne la disponibilité en nutriments, l'influence des apports en eau minéralisée et la variabilité hydrologique.

Le besoin d'intégrer le contexte régional et les conditions hydrologiques dans la restauration des mares minérotrophes

Les mares des tourbières minérotrophes au Canada demeurent peu étudiées (p. ex. Chee et Vitt, 1989; Slack et al., 1980; Sjors, 1959; Vitt et al., 2022), et leur caractérisation floristique en contexte de restauration reste largement inexplorée. Alimentées en partie par des apports minéraux, ces mares présentent des conditions physicochimiques particulières, notamment un pH généralement plus élevé et une disponibilité accrue en nutriments, ce qui influence directement la composition et la structure des assemblages végétaux (Andersen et al., 2011; Schwintzer, 1978; Slack et al., 1980).

Les résultats du Chapitre 2 montrent que la composition de ces communautés varie selon les régions, soulignant l'importance du contexte biogéographique dans les trajectoires de restauration. Ils mettent également en évidence le rôle déterminant des conditions chimiques de l'eau, notamment les concentrations en calcium, azote et phosphore, dans l'établissement de la végétation. Contrairement aux tourbières ombrotrophes, la morphologie des mares ne constitue pas un facteur structurant majeur, alors que la stabilité du niveau d'eau apparaît comme un élément clé reflété sur la végétation colonisatrice. Les mares restaurées, souvent soumises à des fluctuations hydrologiques importantes, offrent des conditions moins favorables à l'établissement d'espèces caractéristiques.

Ces résultats montrent que la restauration des mares minérotrophes nécessite des approches adaptées aux conditions régionales et un contrôle plus fin de l'hydrologie. Ils soulignent également l'importance de la réintroduction active d'espèces ciblées pour favoriser l'établissement des communautés végétales attendues. Au-delà des conditions locales et régionales, ces résultats mettent aussi en évidence le rôle de la structure spatiale des mares restaurées, notamment les gradients de composition des communautés observés en fonction de la distance aux mares.

Le rôle des gradients hydrologiques dans la structuration de la végétation des mares restaurées

Les gradients hydrologiques perpendiculaires aux plans d'eau constituent un élément clé de la structure des écosystèmes, en créant une mosaïque d'habitats favorables à différentes communautés végétales (Wassen et al., 2003; Chen et al., 2015). Les résultats du Chapitre 3 montrent que ces gradients peuvent être partiellement rétablis dans les tourbières ombrotrophes restaurées, contribuant au développement d'une hétérogénéité spatiale importante pour la diversité végétale. Cependant, la composition des communautés ne converge pas entièrement vers celle des mares de référence, ce qui suggère des limites dans les trajectoires de restauration. Ces divergences pourraient être liées à des conditions microtopographiques encore simplifiées et à des

transitions hydrologiques moins marquées entre les zones aquatiques et terrestres, ce qui peut restreindre l'établissement d'espèces caractéristiques des mares naturelles.

Dans ce contexte, les mares spontanées constituent des analogues pertinents de la formation naturelle des mares en tourbière. Leur morphologie et leurs gradients perpendiculaires résultent d'ajustements progressifs aux conditions hydriques et microtopographiques, ce qui favorise l'établissement de communautés végétales plus caractéristiques des systèmes naturels. Elles offrent ainsi un modèle utile pour orienter la conception des mares restaurées.

Ces résultats mettent en évidence que la restauration de l'hétérogénéité spatiale et des gradients de composition des communautés autour des mares constitue un levier important pour améliorer leur qualité écologique. Les résultats suggèrent que des interventions visant à améliorer la disponibilité des propagules ou à ajuster la microtopographie pourraient favoriser l'établissement d'espèces spécialisées et accélérer la convergence vers des états de référence.

Les résultats de cette thèse contribuent à mieux encadrer la restauration des mares en tourbières, tout en mettant en évidence la complexité des processus en jeu et les défis qui persistent. Ces constats soulignent la nécessité de poursuivre les recherches afin de mieux comprendre les trajectoires de restauration et d'optimiser les pratiques mises en œuvre.

Limites et futures recherches

Lors de cette thèse, nous avons identifié plusieurs lacunes de connaissances nécessaires pour comprendre tous les défis et enjeux associés à la colonisation d'espèces végétales des mares. Tout d'abord, une meilleure compréhension de la biologie des espèces végétales associées aux mares apparaît essentielle. En particulier, les mécanismes de dispersion et les capacités d'établissement des espèces demeurent encore peu documentés dans ces écosystèmes. Une meilleure connaissance de ces processus permettrait de développer des stratégies plus efficaces pour favoriser la colonisation des mares restaurées, notamment par la réintroduction ciblée des espèces.

Par ailleurs, cette thèse n'a pas permis d'évaluer de manière détaillée la dynamique du niveau d'eau dans les mares. Or, la variation temporelle de la présence d'eau constitue un facteur clé pour comprendre les conditions d'établissement de la végétation, en particulier dans les mares créées, spontanées et les canaux de drainage. Dans l'ensemble, ces systèmes présentent une forte variabilité hydrologique, pouvant influencer de manière importante les conditions locales d'installation des espèces végétales. Un suivi plus fin de la nappe phréatique et de l'hydropériode permettrait ainsi de mieux cerner l'influence des fluctuations hydrologiques sur la

composition et la survie des communautés végétales, notamment dans les systèmes où la présence d'eau est temporaire.

De plus, les caractéristiques microtopographiques des mares, notamment la pente des berges, ont été considérées de manière qualitative (pentes douces vs abruptes), mais n'ont pas été mesurées de façon quantitative et détaillée. Pourtant, la microtopographie peut influencer les gradients environnementaux et, par conséquent, la présence et la distribution des espèces. Des mesures plus fines et continues de ces caractéristiques permettraient ainsi de mieux comprendre le rôle de la microtopographie dans les trajectoires de restauration.

Concernant les tourbières minérotrophes, le nombre limité de mares de référence échantillonnées a constitué une limite importante. La rareté de ces microformes des régions des tourbières échantillonnées a restreint la capacité à caractériser pleinement la variabilité naturelle des communautés végétales. Un échantillonnage plus étendu permettrait de mieux définir les conditions de référence et d'affiner les objectifs de restauration. Plus largement, les dynamiques écologiques au sein des mares minérotrophes demeurent encore peu étudiées en comparaison des mares ombrotrophes. Approfondir les connaissances sur ces microformes apparaît donc essentiel pour mieux comprendre les processus qui structurent les communautés végétales et améliorer les approches de restauration dans ces milieux.

Il apparait également important de mieux considérer les autres composantes biologiques des mares. Les mares se caractérisent par une forte hétérogénéité environnementale et un isolement relatif (Williams et al., 2003; Biggs et al., 2015), ce qui peut entraîner une grande variabilité dans la composition des communautés entre les sites. Cette variabilité, combinée au rôle des processus stochastiques dans l'assemblage des communautés, complique l'identification des mécanismes de colonisation et de structuration. Une approche intégrée, tenant compte des interactions entre facteurs physico-chimiques, hydrologiques et biologiques, permettrait de mieux comprendre les dynamiques écologiques à l'échelle des mares et d'améliorer les stratégies de restauration.

Enfin, certaines contraintes liées au plan d'échantillonnage doivent être mentionnées. Le nombre inégal de mares échantillonnées entre les différentes catégories a complexifié certaines analyses et limité des comparaisons entre groupes. En particulier, cela n'a pas permis d'inclure les canaux de drainage dans les analyses du troisième chapitre. Une conception d'échantillonnage plus équilibrée faciliterait ainsi les comparaisons entre systèmes et améliorerait la portée des interprétations écologiques des résultats.

Dans l'ensemble, ces limites mettent en évidence la complexité des trajectoires de restauration des mares en tourbières, caractérisées par l'interaction entre conditions environnementales locales, structure des mares et processus de colonisation des espèces. Elles soulignent la nécessité de mieux intégrer ces dimensions dans

les approches de restauration, notamment en combinant des suivis plus fins des gradients hydrologiques et spatiaux, une meilleure caractérisation des microformes, ainsi que des dispositifs d'échantillonnage permettant de comparer plus directement les différents types de mares restaurées et naturelles.

Bibliographie

Aapala, K., Rehell, S., & Similä, M. (2014). Peatland biodiversity. P. 26-32 dans: Ecological Restoration in Drained Peatlands: Best Practices from Finland. Metsähallitus-Natural Heritage Services, Vantaa.

Abdi, H. & Williams, L.J. (2010) Tukey's honestly significant difference (HSD) test. Encyclopedia of Research Design, 3(1), 1–5.

Acuña, V., Hunter, M., & Ruhí, A. (2017). Managing temporary streams and rivers as unique rather than second-class ecosystems. Biological Conservation 211(Part B), 12-19.

Adamec, L. (2020). Biological flora of Central Europe: Utricularia intermedia Hayne, U. ochroleuca R.W. Hartm., U. stygia Thor and U. bremii Heer ex Kölliker. Perspectives in Plant Ecology, Evolution and Systematics, 44, 125520. doi:10.1016/j.ppees.2020.125520.

Alderson, D. M., Evans, M. G., Shuttleworth, E. L., Pilkington, M., Spencer, T., Walker, J., & Allott, T. E. (2019). Trajectories of ecosystem change in restored blanket peatlands. Science of the Total Environment, 665, 785-796.https://doi.org/10.1016/j.scitotenv.2019.02.095

Alexandrov, G.A., Brovkin, V.A., Kleinen, T., Yu, Z., 2020. The capacity of northern peatlands for long-term carbon sequestration. Biogeosciences 17, 47–54. https://doi.org/10.5194/bg-17-47-2020

Allan, J. M., Guêné-Nanchen, M., Rochefort, L., Douglas, D. J., & Axmacher, J. C. (2024). Meta-analysis reveals that enhanced practices accelerate vegetation recovery during peatland restoration. Restoration Ecology, 32(3), e14015. https://doi.org/10.1111/rec.14015

Amacher, M.C., Henderson, R.E., Breithaupt, M.D., Seale, C.L. and LaBauve, J.M. (1990). Unbuffered and buffered salt methods for exchangeable cations and effective cation-exchange capacity. Soil Science Society of America Journal, 54(4), 1036–1042.

Andersen, R., Grasset, L., Thormann, M. N., Rochefort, L., & Francez, A. J. (2010). Changes in microbial community structure and function following Sphagnum peatland restoration. Soil Biology and Biochemistry, 42(2), 291-301.

Andersen, R., Poulin, M., Borcard, D., Laiho, R., Laine, J., Vasander, H. & Tuittila, E.T. (2011). Environmental control and spatial structures in peatland vegetation. Journal of Vegetation Science, 22(5), 878–890.

Andersen, R., Rochefort, L., & Landry, J. (2011). La chimie des tourbières du Québec: une synthèse de 30 années de données. Le Naturaliste canadien, 135(1), 5-14.

Anderson, M. J., & Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs, 83(4), 557–574. https://doi.org/10.1890/12-2010.1

Arlen-Pouliot, Y. and Payette, S. (2015). The influence of climate on pool inception in boreal fens. Botany, 93(10), 637–649.

Armstrong, A., Holden, J., Kay, P., Foulger, M., Gledhill, S., McDonald, A.T., Walker, A. (2009). Drain-blocking techniques on blanket peat: A framework for best practice. Journal of Environmental Management, 90, 3512–3519. https://doi.org/10.1016/j.jenvman.2009.06.003

Arsenault, J., Talbot, J. & Moore, T.R. (2018) Environmental controls of C, N and P biogeochemistry in peatland pools. Science of the Total Environment, 631–632, 714–722. doi:10.1016/j.scitotenv.2018.03.064.

Arsenault, J., Talbot, J., Brown, L. E., Helbig, M., Holden, J., Hoyos-Santillan, J., ... & Lapierre, J. F. (2023). Climate-driven spatial and temporal patterns in peatland pool biogeochemistry. Global Change Biology, 29(14), 4056-4068.

Arsenault, J., Talbot, J., Brown, L.E., Holden, J., Martinez-Cruz, K., Sepulveda-Jauregui, A., Swindles, G.T., Wauthy, M. & Lapierre, J.F. (2022) Biogeochemical distinctiveness of peatland ponds, thermokarst waterbodies, and lakes. Geophysical Research Letters, 49(6), e2021GL097492. doi:10.1029/2021GL097492.

Arsenault, J., Talbot, J., Moore, T. R., Beauvais, M. P., Franssen, J., & Roulet, N. T. (2019). The spatial heterogeneity of vegetation, hydrology and water chemistry in a peatland with open-water pools. Ecosystems, 22(6), 1352-1367.

Arsenault, J., Talbot, J., Moore, T.R., Knorr, K.-H., Teickner, H. & Lapierre, J.-F. (2024) Patterns and drivers of organic matter decomposition in peatland open-water pools. Biogeosciences, 21, 3491–3507. doi:10.5194/bg-21-3491-2024.

Arthington, A. H., Balcombe, S. R., Wilson, G. A., Thoms, M. C., & Marshall, J. (2005). Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. Marine and Freshwater Research, 56(1), 25-35.

Ayotte, G. & Rochefort, L. (2020) Sphagnum mosses of Eastern Canada: Biology—Anatomy—Morphology—Herbarium conservation techniques and microscopic preparations. Montreal: Editions JFD.

Banaå, K. (2013) The hydrochemistry of peatland lakes as a result of the morphological characteristics of their basins. Oceanological and Hydrobiological Studies, 42, 28–39. doi:10.2478/s13545-013-0057-z

Bansal, S., Lishawa, S.C., Newman, S., Tangen, B.A., Wilcox, D., Albert, D. and Windham-Myers, L. et al. (2019). Typha (cattail) invasion in North American wetlands: Biology, regional problems, impacts, ecosystem services, and management. Wetlands, 39(4), 645–684.

Barton, K. (2015) MuMIn: multi-model inference. R package version 1.13.4. Available at: http://r-forge.r-project.org/projects/mumin/ (Accessed: 20 October 2024).

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67, 1-48.

Batzer, D., Wu, H., Wheeler, T., & Eggert, S. (2016). Peatland invertebrates. P. 219-250 dans: Invertebrates in freshwater wetlands: An international perspective on their ecology, Batzer, D. & Boix, D. (éd.), Springer Cham.

Beadle, J.M., Brown, L.E., Holden, J., 2015. Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes. WIREs Water, 2(2), 65-84. https://doi.org/10.1002/WAT2.1063

Belyea, L. R. (2007). Climatic and topographic limits to the abundance of bog pools. Hydrological Processes, 21(5), 675–687. https://doi.org/10.1002/hyp.6275.

Belyea, L. R., & Clymo, R. S. (1998). Do hollows control the rate of peat bog growth? P. 55-65 dans: Patterned mires and mire pools – Origin and development; flora and fauna. Standen, V., Tallis, J. & Meade, R. (éd.), British Ecological Society, Londres.

Belyea, L. R., & Clymo, R. S. (2001). Feedback control of the rate of peat formation. Proceedings of the Royal Society of London. Series B: Biological Sciences, 268(1473), 1315-1321.

Belyea, L.R. & Lancaster, J. (2002) Inferring landscape dynamics of bog pools from scaling relationships and spatial patterns. Journal of Ecology 90(2), doi:10.1046/j.1365-2745.2001.00647.x

Benavides, J. C., & Vitt, D. H. (2014). Response curves and the environmental limits for peat-forming species in the northern Andes. Plant Ecology, 215(9), 937-952.

Benayas, J. M. R., Newton, A. C., Diaz, A., & Bullock, J. M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science, 325(5944), 1121-1124.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P., & Weatherby, A. (2005). 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. Aquatic Conservation: Marine and Freshwater Ecosystems, 15(6), 693-714.

Boix, D., & Batzer, D. (2016). Invertebrate assemblages and their ecological controls across the world's freshwater wetlands. P. 601-639 dans: Invertebrates in freshwater wetlands: An international perspective on their ecology. Batzer, D. & Boix, D. (éd.), Springer Cham.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution, 24(3), 127-135.

Bourgeois, B., Lemay, M. A., Landry, T., Rochefort, L., & Poulin, M. (2019). Seed storage behaviour of eight peatland pool specialists: Implications for restoration. Aquatic Botany, 152, 59-63.

Bourgeois, B., Rochefort, L., Bérubé, V., & Poulin, M. (2018). Response of plant diversity to moss, Carex or Scirpus revegetation strategies of wet depressions in restored fens. Aquatic Botany, 151, 19-24.

Brendonck, L., & Williams, W. D. (2000). Biodiversity in wetlands of dry regions (drylands). P. 181-194 dans: Biodiversity in Wetlands: Assessment, Function and Conservation. Vol. 1. Gopal, B., Junk, W.J. & Davis, T.A. (éd.). Backhuys Publishers, Leiden.

Breton, G., Guêné-Nanchen, M., & Rochefort, L. (2026). Long-term assessment of the Moss Layer Transfer Technique for the restoration of Sphagnum-dominated peatlands. Restoration Ecology, 34(1), e70212.

Brouillet, L., F. Coursol, S.J. Meades, M. Favreau, M. Anions, P. Bélisle, P. Desmet, 2010. VASCAN, the Database of Vascular Plants of Canada [WWW Document]. URL http://data.canadensys.net/vascan/ (consulted on 2024-10-01) (accessed 10.20.24).

Brown, D.H. & Bates, J.W. (1990) Bryophytes and nutrient cycling. Botanical Journal of the Linnean Society, 104(1-3), 129-147. doi:10.1111/j.1095-8339.1990.tb02215.x

Brown, L.E. & Holden, J. (2015) Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes. WIREs Water, 2, 65–84. doi:10.1002/WAT2.1063

Brown, S.M., Petrone, R.M., Mendoza, C. & Devito, K.J. (2010) Surface vegetation controls on evapotranspiration from a sub-humid Western Boreal Plain wetland. Hydrological Processes, 24, 1072–1085. doi:10.1002/hyp.7569.

Bruland, G. L., & Richardson, C. J. (2005). Hydrologic, edaphic, and vegetative responses to microtopographic reestablishment in a restored wetland. Restoration Ecology, 13(3), 515-523.

Bubier, J.L. (1995). The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. Journal of Ecology, 83(3), 403–420.

Butterfield, B. J., & Palmquist, E. C. (2024). Inundation Tolerance, rather than Drought Tolerance, predicts riparian plant distributions along a local hydrologic gradient. Wetlands, 44(1), 6.

Bérubé, V., Rochefort, L., Lavoie, C., 2017. Fen restoration: Defining a reference ecosystem using paleoecological stratigraphy and present-day inventories. Botany 95, 731–750. https://doi.org/10.1139/cjb-2016-0281

Büchi, L. and Vuilleumier, S. (2014). Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. The American Naturalist, 183(5), 612–624.

Calhoun, A. J., Arrigoni, J., Brooks, R. P., Hunter, M. L., & Richter, S. C. (2014). Creating successful vernal pools: a literature review and advice for practitioners. Wetlands, 34(5), 1027-1038.

Calhoun, A. J., Mushet, D. M., Bell, K. P., Boix, D., Fitzsimons, J. A., & Isselin-Nondedeu, F. (2017). Temporary wetlands: challenges and solutions to conserving a 'disappearing' ecosystem. Biological Conservation, 211, 3-11.

Campbell, D. R., Lavoie, C., & Rochefort, L. (2002). Wind erosion and surface stability in abandoned milled peatlands. Canadian Journal of Soil Science, 82(1), 85-95.

Campbell, D.R., Rochefort, L., Lavoie, C., 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. Journal of Applied Ecology 40, 78–91. https://doi.org/10.1046/j.1365-2664.2003.00782.x

Campeau, S., Rochefort, L. and Price, J.S. (2004). On the use of shallow basins to restore cutover peatlands: plant establishment. Restoration Ecology, 12(4), 471–482.

Caners, R. T., Crisfield, V., & Lieffers, V. J. (2019). Habitat heterogeneity stimulates regeneration of bryophytes and vascular plants on disturbed minerotrophic peatlands. Canadian Journal of Forest Research, 49(3), 281-295.

Carlyle, J. C., & Malcolm, D. C. (1986). Larch litter and nitrogen availability in mixed larch–spruce stands. I. Nutrient withdrawal, redistribution, and leaching loss from larch foliage at senescence. Canadian Journal of Forest Research, 16(2), 321-326.

Chapman, P.J., Moody, C.S., Turner, T.E., McKenzie, R., Dinsmore, K.J., Baird, A.J., Billett, M.F., Andersen, R., Leith, F. & Holden, J. (2022) Carbon concentrations in natural and restoration pools in blanket peatlands. Hydrological Processes, 36, e14520. doi:10.1002/hyp.14520

Chapman, S., Buttler, A., Francez, A.-J., Laggoun-Défarge, F., Vasander, H., Schloter, M., Combe, J., Grosvernier, P., Harms, H., Epron, D., Gilbert, D., & Mitchell, E. A. D. (2003). Exploitation of northern peatlands and biodiversity maintenance: A conflict between economy and ecology. Frontiers in Ecology and the Environment, 1(10), 525–532.

Chee, W.-L. & Vitt, D.H. (1989). The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada, Wetlands, 9 227–261. doi: 10.1007/BF03160747.

Chen, X., Li, X., Xie, Y., Li, F., Hou, Z., & Zeng, J. (2015). Combined influence of hydrological gradient and edaphic factors on the distribution of macrophyte communities in Dongting Lake wetlands, China. Wetlands Ecology and Management, 23(3), 481-490.

Cheng, F. Y., Park, J., Kumar, M., & Basu, N. B. (2023). Disconnectivity matters: the outsized role of small ephemeral wetlands in landscape-scale nutrient retention. Environmental Research Letters, 18(2), 024018.

Chimner, R. A., Cooper, D. J., Wurster, F. C., & Rochefort, L. (2017). An overview of peatland restoration in North America: where are we after 25 years? Restoration Ecology, 25(2), 283-292.

Chroňáková, A., Bárta, J., Kaštovská, E., Urbanová, Z., & Picek, T. (2019). Spatial heterogeneity of belowground microbial communities linked to peatland microhabitats with different plant dominants. FEMS Microbiology Ecology, 95(9), fiz130.

Cloutier, V., Lefebvre, R., Savard, M. M., Bourque, É., & Therrien, R. (2006). Hydrogeochemistry and groundwater origin of the Basses-Laurentides sedimentary rock aquifer system, St. Lawrence Lowlands, Québec, Canada. Hydrogeology Journal, 14(4), 573–590. https://doi.org/10.1007/s10040-005-0002-3

Clymo, R. S. (1984) Sphagnum-dominated peat bog: a naturally acid ecosystem. Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 305(1124), 487-499.

Collinge, S. K., Ray, C., & Marty, J. T. (2013). A Long-Term Comparison of Hydrology and Plant Community Composition in Constructed Versus Naturally Occurring Vernal Pools. Restoration Ecology, 21(6), 704–712. https://doi.org/10.1111/rec.12009

Comeau, P.L., Bellamy, D.J., 1986. An ecological interpretation of the chemistry of mire waters from selected sites in eastern Canada. Canadian Journal of Botany 64, 2576–2581. https://doi.org/10.1139/b86-340

Cornell, H. V., & Lawton, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology, 61, 1-12.

Couwenberg, J., Baumann, M., Lamkowski, P., & Joosten, H. (2022). From genes to landscapes: Pattern formation and self-regulation in raised bogs with an example from Tierra del Fuego. Ecosphere, 13(4), e4031.

Crowley, W., Smith, G.F., Mackin, F., Regan, S., Fernandez Valverde, F., Eakin, M. (2021) Recovery of the vegetation of a cutover raised bog in Ireland following rewetting measures. Biology and Environment, 121B, 95–121. doi:10.3318/BIOE.2021.09

Cáceres, M. De & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. Ecology, 90, 3566–3574. doi:10.1890/08-1823.1

da Silveira, F. P., da Silveira, F. F., Porto, A. B., Saraiva, D. D., Overbeck, G. E., & de Chiara Moço, M. C. (2025). Zonation of aquatic plant communities along a flooding gradient in subtropical wetlands. Folia Geobotanica, 59(3), 163-178.

Damman, A.W.H. (1995) Major mire vegetation units in relation to the concepts of ombrotrophy and minerotrophy: A world-wide perspective. Universitetet i Trondheim, Vitenskapsmuseet, Rapport Botanisk Serie, 1994, 1–34.

Davis, J., Pavlova, A., Thompson, R., & Sunnucks, P. (2013). Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Global Change Biology, 19(7), 1970-1984.

Davis, R.B., Anderson, D.S. (2001) Classification and distribution of freshwater peatlands in Maine. Northeastern Naturalist 8(1), 1-50.

Devito, K.J., Hokanson, K.J., Moore, P.A., Kettridge, N., Anderson, A.E., Chasmer, L., Hopkinson, C., Lukenbach, M.C., Mendoza, C.A., Morissette, J., Peters, D.L., Petrone, R.M., Silins, U., Smerdon, B. & Waddington, J.M. (2017). Landscape controls on long-term runoff in sub-humid heterogeneous Boreal Plains catchments. Hydrological Processes, 31(15), 2737–2751. doi: 10.1002/hyp.11213.

Deák, B., Kovács, B., Rádai, Z., Apostolova, I., Kelemen, A., Kiss, R., Lukács, B. A., Török, P., & Valkó, O. (2021). Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. Science of the Total Environment, 763, 144199.

Dibner, R. R., Lawton, C., & Marnell, F. (2014). Reproduction of common frogs, Rana temporaria, in a managed conifer forest and bog landscape in Western Ireland. Herpetological Conservation and Biology, 9(1), 38-47.

DiMauro, D. & Hunter Jr, M.L. (2002) Reproduction of amphibians in natural and anthropogenic temporary pools in managed forests. Forest Science, 48(2), 397–406.

Dinno, A., & Dinno, M. A. (2017). Conover-Iman test of multiple comparisons using rank sums. R project https://cran. r-project. org/web/packages/conover. test/conover. test. pdf.

Dobson, A.J. & Barnett, A.G. (2018) An introduction to generalized linear models. Chapman and Hall/CRC.

Donahue, T., Renou-Wilson, F., Pschenyckyj, C., & Kelly-Quinn, M. (2022). A review of the impact on aquatic communities of inputs from peatlands drained for peat extraction. Biology and Environment Proceedings of the Royal Irish Academy, 122B (3), 145-160.

Douglas, M. M., Bunn, S. E., & Davies, P. M. (2005). River and wetland food webs in Australia's wet–dry tropics: general principles and implications for management. Marine and Freshwater Research, 56(3), 329-342.

Drapeau Picard, A. P., Mazerolle, M. J., Larrivée, M., & Rochefort, L. (2021). Impact of pool design on spider and dytiscid recolonization patterns in a restored fen. Restoration Ecology, 29(5), e13384.

Drexler, J.Z. & Bedford, B.L. (2002) Pathways of nutrient loading and impacts on plant diversity in a New York peatland. Wetlands, 22(2), 263–281.

Environment and Climate Change Canada (2023) [WWW Document]. Available at: https://www.canada.ca/en/environment-climate-change.html (Accessed: 18 August 2024).

Erdős, L., Kröel-Dulay, G., Bátori, Z., Kovács, B., Németh, C., Kiss, P.J. & Tölgyesi, C. (2018). Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. Biological Conservation, 226, 72–80. doi:10.1016/j.biocon.2018.07.029

Evju, M., Hagen, D., Kyrkjeeide, M. O., & Köhler, B. (2020). Learning from scientific literature: can indicators for measuring success be standardized in "on the ground" restoration? Restoration Ecology, 28(3), 519-531.

Faubert, J. (2012) Flore des bryophytes du Québec-Labrador (Vol. 1). Saint-Valérien, Québec: Société québécoise de bryologie.

Ferone, J.M. & Devito, K.J. (2004) Shallow groundwater-surface water interactions in pond-peatland complexes along a Boreal Plains topographic gradient. Journal of Hydrology (Amsterdam), 292, 75–95. doi:10.1016/j.jhydrol.2003.12.032

Filgueiras, B. K., Peres, C. A., Melo, F. P., Leal, I. R., & Tabarelli, M. (2021). Winner–loser species replacements in human-modified landscapes. Trends in Ecology & Evolution, 36(6), 545-555.

Flora of North America Editorial Committee (1993) Flora of North America North of Mexico. New York: Oxford University Press.

Fontaine, N., Poulin, M. & Rochefort, L. (2007) Plant diversity associated with pools in natural and restored peatlands. Mires and Peat, 2(06), 1–17.

Foster, D. R., & Fritz, S. C. (1987). Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. Journal of Ecology, 75, 409-437.

Foster, D. R., & Wright Jr, H. E. (1990). Role of ecosystem development and climate change in bog formation in central Sweden. Ecology, 71(2), 450-463.

Foster, D. R., Wright Jr, H. E., Thelaus, M., & King, G. A. (1988). Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. Journal of Ecology, 76(4), 1164-1185.

Foster, D.R. (1989) REU: Regional, Local and Internal Controls of Raised Bog Development. NSF Award Number 8906386. Directorate for Biological Sciences, 89(8906386), p. 6386.

Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B. & Hudson, J. (2004) Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. Nature, 430(6996), 195–198.

Frolking, S., Talbot, J., Jones, M. C., Treat, C. C., Kauffman, J. B., Tuittila, E. S., & Roulet, N. (2011). Peatlands in the Earth's 21st century climate system. Environmental Reviews, 19(NA), 371-396.

Gagnon, F., Rochefort, L., Lavoie, C., 2018. Spontaneous revegetation of a peatland in Manitoba after peat extraction: diversity of plant assemblages and restoration perspectives. Botany 96, 779–791. https://doi.org/10.1139/cjb-2018-0109

Galatowitsch, S.M., van der Valk, A.G., 1996. Characteristics of recently restored wetlands in the prairie pothole region. Wetlands 16, 75–83. https://doi.org/10.1007/BF03160647

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Restoration Ecology, 27(S1), S1–S46. https://doi.org/10.1111/rec.13035

Gignac, L. D. (1994). Peatland species preferences: an overview of our current knowledge base. Wetlands, 14(3), 216-222.

Gignac, L. D., Vitt, D. H., Zoltai, S. C., & Bayley, S. E. (1991). Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. Nova Hedwigia, 53(1-2), 27-71.

Gilbert, D., Francez, A.-J., Amblard, C., & Bourdier, G. (1999). The microbial communities at the surface of the Sphagnum peatlands: good indicators of human disturbances? Ecologie, 30(1), 45-52.

Glaser, P. H. (1992). Ecological Development. In: The patterned peatlands of Minnesota, Wright, H.E., Coffin, B., Aaseng, N.E. (eds.).

Glaser, P. H., & Janssens, J. A. (1986). Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. Canadian Journal of Botany, 64(2), 395-415.

Glaser, P.H., Hansen, B.C., Siegel, D.I., Reeve, A.S. and Morin, P.J. (2004). Rates, pathways and drivers for peatland development in the Hudson Bay Lowlands, northern Ontario, Canada. Journal of Ecology, 92(6), 1036–1053.

Godoy, O., Soler-Toscano, F., Portillo, J. R., & Langa, J. A. (2024). The assembly and dynamics of ecological communities in an ever-changing world. Ecological Monographs, 94(4), e1633.

González del Tánago, M., García de Jalón, D., & Román, M. (2012). River restoration in Spain: theoretical and practical approach in the context of the European Water Framework Directive. Environmental Management, 50(1), 123-139.

González, E. & Rochefort, L. (2014) Drivers of success in 53 cutover bogs restored by a moss layer transfer technique. Ecological Engineering, 68, 279–290.

González, E., & Rochefort, L. (2019). Declaring success in Sphagnum peatland restoration: Identifying outcomes from readily measurable vegetation descriptors. Mires and Peat, 24, Article 19, 1–16. doi: 10.19189/MaP.2017.OMB.305

González, E., Rochefort, L., Boudreau, S. & Poulin, M. (2014) Combining indicator species and key environmental and management factors to predict restoration success of degraded ecosystems. Ecological Indicators, 46, 156–166. doi:10.1016/j.ecolind.2014.06.016

González-Megías, A., María Gómez, J., & Sánchez-Piñero, F. (2007). Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography, 30(1), 31-41.

Goodbrand, A., Westbrook, C. J., & Van der Kamp, G. (2019). Hydrological functions of a peatland in a Boreal Plains catchment. Hydrological Processes, 33(4), 562-574.

Gorham, E. (1991). Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications, 1(2), 182-195.

Grace, J. B., & Wetzel, R. G. (1981). Habitat Partitioning and Competitive Displacement in Cattails (Typha): Experimental Field Studies. The American Naturalist, 118(4), 463–474.

Graf, M. D., & Rochefort, L. (2016). A conceptual framework for ecosystem restoration applied to industrial peatlands. Peatland restoration and ecosystem services: Science, policy and practice, 192-212.

Graf, M. D., Rochefort, L., & Poulin, M. (2008). Spontaneous revegetation of cutaway peatlands of North America. Wetlands, 28(1), 28-39.

Graf, M., Rochefort, L., (2009). Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands. Écoscience 16, 158–166. https://doi.org/10.2980/16-2-3128

Graf, M.D. & Rochefort, L. (2016) A conceptual framework for ecosystem restoration applied to industrial peatlands. in: Peatland Restoration and Ecosystem Services, Cambridge University Press, 192–212. doi:10.1017/CBO9781139177788.012

Graf, M.D., Rochefort, L., Poulin, M., 2008. Spontaneous revegetation of cutaway peatlands of North America. Wetlands 28, 28–39. https://doi.org/10.1672/06-136.1

Graham, J. D., Glenn, N. F., Spaete, L. P., & Hanson, P. J. (2020). Characterizing peatland microtopography using gradient and microform-based approaches. Ecosystems, 23(7), 1464-1480.

Graham, L. L. B., & Page, S. E. (2018). A limited seed bank in both natural and degraded tropical peat swamp forest: the implications for restoration. Mires and Peat, 22, Article 02, 1–13. doi: 10.19189/MaP.2017.OMB.302

Groeneveld, E. V., & Rochefort, L. (2002). Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems. Suo, 53(3-4), 73-85.

Groeneveld, E., & Rochefort, L. (2005). Polytrichum strictum as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. Restoration Ecology, 13(1), 74-82.

Groves, C.R. and Game, E.T. (2016) Conservation planning: informed decisions for a healthier planet. Denver, CO: Roberts and Company Publishers.

Haapalehto, T. O., Vasander, H., Jauhiainen, S., Tahvanainen, T., & Kotiaho, J. S. (2011). The Effects of Peatland Restoration on Water-Table Depth, Elemental Concentrations, and Vegetation: 10 Years of Changes. Restoration Ecology, 19(5), 587–598. https://doi.org/10.1111/j.1526-100X.2010.00704.x

Haapalehto, T., Juutinen, R., Kareksela, S., Kuitunen, M., Tahvanainen, T., Vuori, H., & Kotiaho, J. S. (2017). Recovery of plant communities after ecological restoration of forestry-drained peatlands. Ecology and Evolution, 7(19), 7848-7858.

Haapalehto, T., Kotiaho, J.S., Matilainen, R. & Tahvanainen, T. (2014) The effects of long-term drainage and subsequent restoration on water table level and pore water chemistry in boreal peatlands. Journal of Hydrology (Amsterdam), 519, 1493–1505. doi:10.1016/j.jhydrol.2014.09.013

Hamilton, J. D., Kelly, C. A., Rudd, J. W., Hesslein, R. H., & Roulet, N. T. (1994). Flux to the atmosphere of CH4 and CO2 from wetland ponds on the Hudson Bay lowlands (HBLs). Journal of Geophysical Research: Atmospheres, 99(D1), 1495-1510.

Harris, L. I., Richardson, K., Bona, K. A., Davidson, S. J., Finkelstein, S. A., Garneau, M., McLaughlin, J., Nwaishi, F., Olefeldt, D., Packalen, M., Roulet, N. T., Southee, F. M., Strack, M., Webster, K. L., Wilkinson, S. L., & Ray, J. C. (2022). The essential carbon service provided by northern peatlands. Frontiers in Ecology and the Environment, 20(4), 222–230.

Hartsock, J. A., House, M., Clark, M. G., & Vitt, D. H. (2021). A comparison of plant communities and water chemistry at Sandhill Wetland to natural Albertan peatlands and marshes. Ecological Engineering, 169. https://doi.org/10.1016/j.ecoleng.2021.106313

Hassanpour Fard, G., Farries, E., Bérubé, V., Rochefort, L., Strack, M., 2020. Key Species Superpose the Effect of Species Richness and Species Interaction on Carbon Fluxes in a Restored Minerotrophic Peatland. Wetlands 40, 333–349. https://doi.org/10.1007/s13157-019-01176-5

Hautier, Y., Niklaus, P.A. & Hector, A. (2009) Competition for light causes plant biodiversity loss after eutrophication. Science, 324, 636–638. doi:10.1126/science.1169640

Holden, J. (2004). Hydrological connectivity of soil pipes determined by ground-penetrating radar tracer detection. Earth Surface Processes and Landforms, 29(4), 437-442.

Holden, J., Evans, M.G., Burt, T.P. & Horton, M. (2006) Impact of land drainage on peatland hydrology. Journal of Environmental Quality, 35, 1764–1778. doi:10.2134/jeq2005.0477

Holden, J., Green, S. M., Baird, A. J., Grayson, R. P., Dooling, G. P., Chapman, P. J., Evans, C. D., Peacock, M., Swindles, G. T., & Brown, L. E. (2017). The impact of ditch blocking on the hydrological functioning of blanket peatlands. Hydrological Processes, 31(3), 525–539.

Holden, J., Moody, C. S., Edward Turner, T., McKenzie, R., Baird, A. J., Billett, M. F., Chapman, P. J., Dinsmore, K. J., Evans, C. D., Grayson, R. P., Jones, T., Kaduk, J., Levy, P. E., Matthews, R., McNamara, N. P., Parry, L. E., Ritson, J. P., & Dooling, G. (2018). Water-level dynamics in natural and artificial pools in blanket peatlands. Hydrological Processes, 32(4), 550–561.

Holl, K.D., Luong, J.C. & Brancalion, P.H.S. (2022) Overcoming biotic homogenization in ecological restoration. Trends in Ecology & Evolution, 37, 777–788. doi:10.1016/j.tree.2022.05.002

Hugron, S., Guene-Nanchen, M., Roux, N., LeBlanc, M. C., & Rochefort, L. (2020). Plant reintroduction in restored peatlands: 80% successfully transferred–Does the remaining 20% matter? Global Ecology and Conservation, 22, e01000.

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

Hunter, M.L., 2005. A mesofilter conservation strategy to complement fine and coarse filters. Conservation Biology, 19, 1025–1029.

Ingram, H. A. P. (1982). Size and shape in raised mire ecosystems: a geophysical model. Nature, 297(5864), 300-303.

Janzen, D.H. & Vázquez-Yanes, C. (1991) Aspects of tropical seed ecology of relevance to management of tropical forest wildlands. In: Gómez-Pompa, A., Whitmore. T.C. & Hadley, M. (eds.) Rain Forest Regeneration and Management, Parthenon, Carnforth, xxiii+457 pp.

Jean, M., Bouchard, A., (1993). Riverine wetland vegetation: importance of small-scale and large-scale environmental variation. Journal of Vegetation Science 4, 609–620. https://doi.org/10.2307/3236126

Johansen, M.D., Aker, P., Klanderud, K., Olsen, S.L. & Skrindo, A.B. (2017) Restoration of peatland by spontaneous revegetation after road construction. Applied Vegetation Science, 20, 631–640. doi:10.1111/avsc.12329

Jolin, É., Arsenault, J., Talbot, J., Hassan, M. & Rochefort, L. (2024) Are pools created when restoring extracted peatlands biogeochemically similar to natural peatland pools? Ecological Applications, 34(8), e3052. doi:10.1002/eap.3052

Jones, J.M., Massicotte, H.B. & Fredeen, A.L. (2016). Calcium and pH co-restrict abundance of Drosera rotundifolia (Droseraceae) in a Sphagnum bog in central British Columbia. Botany, 94(2), 139–146. doi:10.1139/cjb-2015-0185.

Joosten, H., & Clarke, D. (2002). Wise use of mires and peatlands: background and principles including a framework for decision-making. International Peat Society, Jyväskylä; International Mire Conservation Group, Greifswald.

Juutinen, S., Moore, T. R., Bubier, J. L., Arnkil, S., Humphreys, E., Marincak, B., Roy, C., & Larmola, T. (2018) Long-term nutrient addition increased CH_4 emission from a bog through direct and indirect effects. Scientific Reports, 8, 3838. https://doi.org/10.1038/s41598-018-22210-2

Karofeld, E. (1998). The dynamics of the formation and development of hollows in raised bogs in Estonia. The Holocene, 8(6), 697-704.

Karofeld, E., & Toom, M. (1999). Mud-bottoms in Mannikjarve bog, central Estonia. In Proceedings of the Estonian Academy of Science Biology Ecology (Vol. 48, 216-235).

Karofeld, E., & Tõnisson, H. (2014). Spatio-temporal changes in bog pool bottom topography–temperature effect and its influence on pool development: an example from a raised bog in Estonia. Hydrological Processes, 28(3), 958-968.

Karofeld, E., Kasemets, M., Szava-Kovats, R., & Tõnisson, H. (2008). Does anticipated warming accelerate bog pool bottom rise, topographic changes and related peat decomposition. In 13th International Peat Congress, Farrell C, Feehan J (eds). University College Dublin, International Peat Society: Tullamore (587-591).

Kasimir, Å., He, H., Jansson, P.-E., Lohila, A., & Minkkinen, K. (2021). Mosses are Important for Soil Carbon Sequestration in Forested Peatlands. Frontiers in Environmental Science, 9. https://doi.org/10.3389/fenvs.2021.680430

Kassambara, A., Mundt, F., 2017. Package. factoextra.' Extract and visualize the results of multivariate data analyses 76.

Keddy, P. A. (2010). Wetland ecology: principles and conservation. Cambridge university press.

Keightley, A. T., Osborne, A. W., & Rogers, T. (2025). Cutting Juncus: Management of dense rush to encourage Sphagnum establishment on an ex-milled peatland. Mires and Peat, 32, 35. https://doi.org/10.19189/001c.154768

Kennedy, G. & Mayer, T. (2002) Natural and constructed wetlands in Canada: An overview. Water Quality Research Journal, 37(2), 295–325

Khan, A. S., Guêné-Nanchen, M., & Rochefort, L. (2025). Unfolding a peatland's story: Assessing the restoration outcomes and driving factors from a disturbed minerotrophic peatland in Eastern Canada. Ecological Engineering, 212, 107496.

Kivimäki, S.K., Yli-Petäys, M. & Tuittila, E.S. (2008) Carbon sink function of sedge and Sphagnum patches in a restored cut-away peatland: Increased functional diversity leads to higher production. Journal of Applied Ecology, 45, 921–929. doi:10.1111/j.1365-2664.2008.01458.x

Koivunen, I., Muotka, T., Jokikokko, M., Virtanen, R., & Jyväsjärvi, J. (2023). Downstream impacts of peatland drainage on headwater stream biodiversity and ecosystem functioning. Forest Ecology and Management, 543, 121143.

Kooijman, A., Hedenäs, L., 2009. Changes in nutrient availability from calcareous to acid wetland habitats with closely related brown moss species: increase instead of decrease in N and P. Plant Soil 324, 267–278. https://doi.org/10.1007/s11104-009-9954-8

Laberge, V., Hugron, S., Rochefort, L. & Poulin, M. (2015) Influence of different bryophyte carpets on vascular plant establishment around pools in restored peatlands. Land Degradation & Development, 26, 813–818. doi:10.1002/ldr.2243

Lachance, D., Fortin, G. et Dufour Tremblay, G. (2021) Identification et délimitation des milieux humides du Québec méridional – version décembre 2021. Québec : Ministère de l'Environnement et de la Lutte contre les changements climatiques, Direction adjointe de la conservation des milieux humides. Available online: https://www.environnement.gouv.qc.ca/eau/rives/guide-identif-dellimit-milieux-humides.pdf.

Lamers, L. P. M., Vile, M. A., Grootjans, A. P., Acreman, M. C., van Diggelen, R., Evans, M. G., Richardson, C. J., Rochefort, L., Kooijman, A. M., Roelofs, J. G. M., & Smolders, A. J. P. (2015). Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. Biological Reviews of the Cambridge Philosophical Society, 90(1), 182–203. https://doi.org/10.1111/brv.12102

Landry, J. & Rochefort, L. (2011) Le drainage des tourbières: impacts et techniques de remouillage. Groupe de recherche en écologie des tourbières, Université Laval, Québec.

Landry, T., Rochefort, L., & Poulin, M. (2012). Impact of seedbed and water level on the establishment of plant species associated with bog pools. Native Plants Journal, 13(3), 205-215.

Lane, I. G., Portman, Z. M., Herron-Sweet, C. H., Pardee, G. L., & Cariveau, D. P. (2022). Differences in bee community composition between restored and remnant prairies are more strongly linked to forb community differences than landscape differences. Journal of Applied Ecology, 59(1), 129-140.

Larkin, D.J., Bruland, G.L., Zedler, J.B., 2016. Heterogeneity Theory and Ecological Restoration, in: Foundations of Restoration Ecology. Island Press/Center for Resource Economics, Washington, DC, 271–300. https://doi.org/10.5822/978-1-61091-698-1_10

Larmola, T., Bubier, J.L., Kobyljanec, C., Basiliko, N., Juutinen, S., Humphreys, E., Preston, M. & Moore, T.R. (2013) Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog. Global Change Biology, 19, 3729–3739. Available at: https://doi.org/10.1111/gcb.12328

Lavoie, C., Grosvernier, P., Girard, M. & Marcoux, K. (2003) Spontaneous revegetation of mined peatlands: an useful restoration tool? Wetlands Ecology and Management, 11, 97–107.

Lavoie, C., Saint-Louis, A. & Lachance, D. (2005) Vegetation dynamics on an abandoned vacuum-mined peatland: 5 years of monitoring. Wetlands Ecology and Management, 13, 621–633.

Lemmer, M., Xu, B., Strack, M. & Rochefort, L. (2023) Reestablishment of peatland vegetation following surface leveling of decommissioned in situ oil mining infrastructures. Restoration Ecology, 31(3): e13714; DOI: 10.1111/rec.13714.

Locky, D.A., Bayley, S.E., 2006. Plant diversity, composition, and rarity in the southern boreal peatlands of Manitoba, Canada. Canadian Journal of Botany 84, 940–955. https://doi.org/10.1139/b06-049

Lenssen, J., Menting, F., van der Putten, W., & Blom, K. (1999). Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. Oikos, 86(3), 523-534.

Li, J., Li, M., Zhao, L., Sun, X., Gao, M., Sheng, L., & Bian, H. (2022). Characteristics of soil carbon emissions and bacterial community composition in peatlands at different stages of vegetation succession. Science of the Total Environment, 839, 156242.

Lichvar, R.W., Melvin, N.C., Butterwick, M.L. et Kirchner, W.N. (2012) National Wetland Plant List Indicator Rating Definitions. ERDC/CRREL TN-12-1. Hanover, NH: U.S. Army Engineer Research and Development Center Cold Regions Research and Engineering Laboratory. Available online: https://wetland-plants.usace.army.mil/static/references/NWPL/pubs/2012b_Lichvar_et_al.pdf

Limpens, J., Berendse, F. & Klees, H. (2003) N deposition affects N availability in interstitial water, growth of Sphagnum and invasion of vascular plants in bog vegetation. New Phytologist, 157, 339–347.

Lindsay, R. (2010) Peatbogs and carbon: a critical synthesis to inform policy development in oceanic peat bog conservation and restoration in the context of climate change. University of East London, Environmental Research Group.

Lindsay, R., Campus, S., & Lane, W. (2010). Peatbogs and carbon: a critical synthesis to inform policy development in oceanic peat bog conservation and restoration in the context of climate change. RSPB Scotland, 315.

Little-Devito, M. (2024) Impacts on water quality at a newly opened and extracted peatland: Influence of internal processes and hydrological connectivity in horticultural peat harvesting. MSc thesis, University of Alberta, Edmonton, Alberta.

Liu, W., Liu, G., & Zhang, Q. (2014). Shoreline vegetation in the Danjiangkou Reservoir: characteristics, related factors, and differences with adjacent riverine wetlands. CLEAN–Soil, Air, Water, 42(7), 1014-1021.

Lovadi, I., Ifadatin, S. and Andarisko, B. (2023). Preliminary study on the man-made habitat of Utricularia gibba L. in the tropical peatland environment. IOP Conference Series: Earth and Environmental Science, 1266(1), p. 012009. IOP Publishing. doi:10.1088/1755-1315/1266/1/012009.

Lundquist, C. J., Bulmer, R. H., Clark, M. R., Hillman, J. R., Nelson, W. A., Norrie, C. R., Olds, A. D., Thrush, S. F., & Hewitt, J. E. (2017). Challenges for the conservation of marine small natural features. Biological Conservation, 211, 69–79.

Luo, W., Song, F., & Xie, Y. (2008). Trade-off between tolerance to drought and tolerance to flooding in three wetland plants. Wetlands, 28(3), 866-873.

Magurran, A. E. (2005). Biological diversity. Current Biology, 15(4), R116-R118.

Mallik, A. U., Lamb, E. G., & Rasid, H. (2001). Vegetation zonation among the microhabitats in a lacustrine environment: analysis and application of belowground species trait patterns. Ecological Engineering, 18(2), 135-146.

Martinez Arbizu, P., 2020. Pairwise Adonis: Pairwise multilevel comparison using adonis [WWW Document]. R package version 0.4, 1.

Mazerolle, M. J. (2005). Peatlands and green frogs: A relationship regulated by acidity? Ecoscience, 12(1), 60-67.

Mazerolle, M.J., Desrochers, A. & Rochefort, L. (2005) Landscape characteristics influence pond occupancy by frogs after accounting for detectability. Ecological Applications, 15(3), 824-834

Mazerolle, M.J., Poulin, M., Lavoie, C., Rochefort, L., Desrochers, A. & Drolet, B. (2006) Animal and vegetation patterns in natural and man-made bog pools: implications for restoration. Freshwater Biology, 51, 333-350. https://doi.org/10.1111/j.1365-2427.2005.01480.x

McCarter, C. P., & Price, J. S. (2015). The hydrology of the Bois-des-Bel peatland restoration: hydrophysical properties limiting connectivity between regenerated Sphagnum and remnant vacuum harvested peat deposit. Ecohydrology, 8(2), 173-187.

McCorry, M. J., & Renou, F. (2003). Ecology and management of Juncus effusus (soft rush) on cutaway peatlands. Forest Ecosystem Research Group Report, 69, 66.

McEnroe, N. A., Roulet, N. T., Moore, T. R., & Garneau, M. (2009). Do pool surface area and depth control CO2 and CH4 fluxes from an ombrotrophic raised bog, James Bay, Canada?. Journal of Geophysical Research: Biogeosciences, 114(G1).

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution, 14(11), 450-453.

McKnight, P. E., & Najab, J. (2010). Mann-Whitney U test. P. In: The Corsini Encyclopedia of Psychology. Weiner, I.B. and Craighead, W.E. (eds.). https://doi.org/10.1002/9780470479216.corpsy0524.

McNaughton, S.J. (1968) Structure and function in California grasslands. Ecology, 49, 962–972. https://doi.org/10.2307/1936547.

Meeker, J.E., Wilcox, D.A., Johnson, S.E. & Tillison, N. (2023). Tracking vegetation transitions due to invasion of cattail (Typha) in Lake Superior coastal peatlands. Wetlands, 43(2), 18. doi: 10.1007/s13157-023-01664-9.

Merritt, D. M., Nilsson, C., & Jansson, R. (2010). Consequences of propagule dispersal and river fragmentation for riparian plant community diversity and turnover. Ecological Monographs, 80(4), 609-626.

Merritt, D. M., Scott, M. L., LeRoy Poff, N., Auble, G. T., & Lytle, D. A. (2010). Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. Freshwater Biology, 55(1), 206-225.

Middleton, B., van Diggelen, R. & Jensen, K. (2006) Seed dispersal in fens. Applied Vegetation Science, 9(2), 279–284.

Miller, B. P., Sinclair, E. A., Menz, M. H., Elliott, C. P., Bunn, E., Commander, L. E., Hobbs, R. J., Kettenring, K. M., Prober, S. M., Robertson, M. P., Smith, C. S., Staggemeier, V. G., van der Meer, P. J., & Stevens, J. C. (2017). A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. Restoration Ecology, 25(4), 605–617.

Minasny, B., Adetsu, D. V., Aitkenhead, M., Artz, R. R. E., Baggaley, N., Barthelmes, A., Beucher, A., Caron, J., Conchedda, G., Connolly, J., Deragon, R., Evans, C., Fadnes, K., Fiantis, D., Gagkas, Z., Gilet, L., Gimona, A., Glatzel, S., Greve, M. H., Grzybowski, M., Hrbáček, F., Hugelius, G., Järveoja, J., Kasimir, Å., Knadel, M., Kreyling, J., Krüger, J. P., Lamers, L. P. M., Lamentowicz, M., Lindsay, R., Lohila, A., Lunina, O., Marttila, H., McCarter, C. P. R., McKenzie, R., Miettinen, J., Miller, C. J., Nilsson, M. B., Noble, A., O'Sullivan, L., Page, S. E., Peacock, M., Petrescu, A. M. R., Poulin, M., Qiu, C., Ratcliffe, J. L., Reiche, M., Rydin, H., Talbot, J., Tanneberger, F., Tuittila, E.-S., Venäläinen, A., Vesala, T., Vikman, J., Webster, K. L., Waddington, J. M., Wilson, D., & Zak, D. (2024). Mapping and monitoring peatland conditions from global to field scale. Biogeochemistry, 167, 383–425.

Minkkinen, K. and Laine, J. (2006) Vegetation heterogeneity and ditches create spatial variability in methane fluxes from peatlands drained for forestry. Plant and Soil, 285, 289–304. https://doi.org/10.1007/s11104-006-9016-4

Molina, J. A., & Navarro, G. (2025). Plant zonation patterns along the water-level gradient in two high-elevation wetlands under different macroclimates. Harvard Papers in Botany, 30(1), 61-74.

Moore, T.R., Trofymow, J.A., Siltanen, M. & Kozak, L.M. (2008) Litter decomposition and nitrogen and phosphorus dynamics in peatlands and uplands over 12 years in central Canada. Oecologia, 157, 317–325. https://doi.org/10.1007/s00442-008-1076-0

Moreno-Mateos, D., Alberdi, A., Morriën, E., van der Putten, W. H., Rodríguez-Uña, A., & Montoya, D. (2020). The long-term restoration of ecosystem complexity. Nature Ecology & Evolution, 4(5), 676-685.

Morin, N. R. (2000). Flora of North America. Oxford University Press.

Mosanghini, D., Oriolo, G., & Boscutti, F. (2023). Different ways to success: Plant community trajectories over time and a soil moisture gradient in restored wetlands. Journal of Applied Ecology, 60(1), 29-40.

Muench, A. and Elsey-Quirk, T. (2019). Competitive reversal between plant species is driven by species-specific tolerance to flooding stress and nutrient acquisition during early marsh succession. Journal of Applied Ecology, 56(9), 2236–2247.

Murtagh, F., & Legendre, P. (2014). Ward's hierarchical agglomerative clustering method: which algorithms implement Ward's criterion? Journal of Classification, 31(3), 274-295.

Måren, I.E., Kapfer, J., Aarrestad, P.A., Grytnes, J., Vandvik, V., 2018. Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient. Ecology 99, 148–157. https://doi.org/10.1002/ecy.2052

Nakagawa, S., Johnson, P. C., & Schielzeth, H. (2017). The coefficient of determination R 2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society Interface, 14(134), 20170213.

National Wetlands Working Group (1997) The Canadian Wetland Classification System, 2nd ed. Warner, B.G. et Rubec, C.D.A. (eds), Wetlands Research Centre, Université de Waterloo, Waterloo, ON.

Nichols, J. E., & Peteet, D. M. (2019). Rapid expansion of northern peatlands and doubled estimate of carbon storage. Nature Geoscience, 12(11), 917-921.

Noleto, E. V., Barbosa, M. V. M., & Pelicice, F. M. (2019). Distribution of aquatic macrophytes along depth gradients in Lajeado Reservoir, Tocantins River, Brazil. Acta Limnologica Brasiliensia, 31, e6.

Nugent, C., Kanali, C., Owende, P. M., Nieuwenhuis, M., & Ward, S. (2003). Characteristic site disturbance due to harvesting and extraction machinery traffic on sensitive forest sites with peat soils. Forest Ecology and Management, 180(1-3), 85-98.

Nugent, K. A., Strachan, I. B., Strack, M., Roulet, N. T., & Rochefort, L. (2018). Multi-year net ecosystem carbon balance of a restored peatland reveals a return to carbon sink. Global Change Biology, 24(12), 5751–5768. https://doi.org/10.1111/gcb.14449

Nungesser, M. K. (2011). Reading the landscape: temporal and spatial changes in a patterned peatland. Wetlands Ecology and Management, 19(6), 475-493.

Oksanen, J. & Simpson, G.L. (2009) The vegan Package. R package version 2.6-5. Available at: https://github.com/vegandevs/vegan (Accessed: 20 October 2024).

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H.H., Barbour, M.T., Bedward, M., Bolker, B.M., Brocard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., & Ter Braak, C. (2024) 'Vegan: Community Ecology Package. R package version 2.6-5. Available at: https://github.com/vegandevs/vegan (Accessed: 20 October 2024).

Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution, 19(1), 18-24.

Pace, M. L. & Prairie, Y. T. (2005). Respiration in lakes. Pp. 1013-122 in: Respiration in Aquatic Ecosystems, del Giorgio, P. & Williams, P. (eds.). Oxford University Press, Oxford.

Paillex, A., Dolédec, S., Castella, E., Mérigoux, S., & Aldridge, D. C. (2013). Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. Journal of Applied Ecology, 50(1), 97-106.

Pasquet, S., Pellerin, S., & Poulin, M. (2015). Three decades of vegetation changes in peatlands isolated in an agricultural landscape. Applied Vegetation Science, 18(2), 220-229.

Payette, S., & Rochefort, L. (éd.) (2001). Écologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, Québec. 621 p.

Peacock, M., Evans, C.D., Fenner, N. & Freeman, C. (2013) Natural revegetation of bog pools after peatland restoration involving ditch blocking—The influence of pool depth and implications for carbon cycling. Ecological Engineering, 57, 297–301. https://doi.org/10.1016/j.ecoleng.2013.04.055

Pearsall, W. H. (1956). Two blanket-bogs in Sutherland. Journal of Ecology, 44(2), 493-516.

Pellerin, S., & Poulin, M. (2013). Analyse de la situation des milieux humides au Québec et recommandations à des fins de conservation et de gestion durable. Rapport final pour le Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, Montréal, Québec.

Pellerin, S., Lagneau, L. A., Lavoie, M., & Larocque, M. (2009). Environmental factors explaining the vegetation patterns in a temperate peatland. Comptes Rendus Biologies, 332(8), 720-731.

Pinceloup, N., Poulin, M., Brice, M.-H. & Pellerin, S. (2020) Vegetation changes in temperate ombrotrophic peatlands over a 35 year period. PLOS One, 15, e0229146. https://doi.org/10.1371/journal.pone.0229146

Pinto-Ledezma, J.N., Larkin, D.J. & Cavender-Bares, J. (2018) Patterns of beta diversity of vascular plants and their correspondence with biome boundaries across North America. Frontiers in Ecology and Evolution, 6, 194. https://doi.org/10.3389/fevo.2018.00194

Poschlod, P. & Braun-Reichert, R. (2017) Small natural features with large ecological roles in ancient agricultural landscapes of Central Europe - history, value, status, and conservation. Biological Conservation, 211, 60–68. https://doi.org/10.1016/j.biocon.2016.12.016

Poulin, M., Andersen, R., & Rochefort, L. (2013). A new approach for tracking vegetation change after restoration: a case study with peatlands. Restoration Ecology, 21(3), 363-371.

Poulin, M., Careau, D., Rochefort, L. & Desrochers, A. (2002) From satellite imagery to peatland vegetation diversity: how reliable are habitat maps? Conservation Ecology, 6(2), Article 16. https://www.ecologyandsociety.org/vol6/iss2/art16/

Poulin, M., Rochefort, L., & Desrochers, A. (1999). Conservation of bog plant species assemblages: Assessing the role of natural remnants in mined sites. Applied Vegetation Science, 2(2), 169–180. https://doi.org/10.2307/1478980

Poulin, M., Rochefort, L., Pellerin, S. & Thibault, J. (2004) Threats and protection for peatlands in Eastern Canada. Géocarrefour, 79, 331–344. https://doi.org/10.4000/geocarrefour.875

Poulin, M., Rochefort, L., Quinty, F. & Lavoie, C. (2005) Spontaneous revegetation of mined peatlands in eastern Canada. Canadian Journal of Botany, 83, 539–557. https://doi.org/10.1139/b05-025

Pouliot, R., Rochefort, L., & Karofeld, E. (2011). Initiation of microtopography in revegetated cutover peatlands. Applied Vegetation Science, 14(2), 158-171.

Prausová, R., Holzbauerová, H., Špringrová, I., Jará, N., Šafářová, L., Cross, A. T., & Adamec, L. (2022). Seed germination ecology of common bladderwort (Utricularia vulgaris L.). Aquatic Botany, 182. https://doi.org/10.1016/j.aquabot.2022.103545

Price, J. S. (1996). Hydrology and microclimate of a partly restored cutover bog, Quebec. Hydrological Processes, 10(10), 1263-1272.

Price, J. S. (2003). Role and character of seasonal peat soil deformation on the hydrology of undisturbed and cutover peatlands. Water Resources Research, 39(9), 1241. doi:10.1029/2002WR001302.

Price, J. S., Heathwaite, A. L., & Baird, A. J. (2003). Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetlands Ecology and Management, 11(1), 65-83.

Prijac, A., Gandois, L., Jeanneau, L., Taillardat, P. & Garneau, M. (2022) Dissolved organic matter concentration and composition discontinuity at the peat–pool interface in a boreal peatland. Biogeosciences, 19, 4571–4588. https://doi.org/10.5194/bg-19-4571-2022

Qi, Q., Zhang, D., Zhang, M., Tong, S., An, Y., Wang, X., & Zhu, G. (2021). Hydrological and microtopographic effects on community ecological characteristics of Carex schmidtii tussock wetland. Science of the Total Environment, 780, 146630.

Qualls, R.G., 1989. The biogeochemical properties of dissolved organic matter in a hardwood forest ecosystem: Their influence on the retention of nitrogen, phosphorus, and carbon. University of Georgia, Georgia.

Quinton, W.L. & Roulet, N.T. (1998) Spring and summer runoff hydrology of a subarctic patterned wetland. Arctic and Alpine Research, 30(3), 285–294. https://doi.org/10.1080/00040851.1998.12002902

Quinty, F. & Rochefort, L. (2003) Peatland restoration guide, 2nd ed. Canadian Sphagnum Peat Moss Association et New Brunswick Department of Natural Resources and Energy. Quebec City, Québec.

Quinty, F., LeBlanc, M.C. & Rochefort, L. (2019) Peatland restoration guide – Plant material collecting and donor site management. Peatland Ecology Research Group, Canadian Sphagnum Peat Moss Association and Association des producteurs de tourbe horticole du Québec. Quebec City, Québec.

Quinty, F., LeBlanc, M.C. & Rochefort, L. (2020a) Peatland restoration guide – Planning restoration projects. Peatland Ecology Research Group, Canadian Sphagnum Peat Moss Association and Association des producteurs de tourbe horticole du Québec. Quebec City, Québec.

Quinty, F., LeBlanc, M.C. & Rochefort, L. (2020b) Peatland restoration guide – Site preparation and rewetting. Peatland Ecology Research Group, Canadian Sphagnum Peat Moss Association and Association des producteurs de tourbe horticole du Québec. Quebec City, Québec.

Quinty, F., LeBlanc, M.C. & Rochefort, L. (2020c) Peatland restoration guide – Spreading of plant material, mulch and fertilizer. Peatland Ecology Research Group, Canadian Sphagnum Peat Moss Association and Association des producteurs de tourbe horticole du Québec. Quebec City, Québec.

R core team, 2022. R foundation for statistical computing [WWW Document]. URL https://www.R-project.org/. (accessed 2.18.25).

Raulings, E. J., Morris, K. A. Y., Roache, M. C., & Boon, P. I. (2010). The importance of water regimes operating at small spatial scales for the diversity and structure of wetland vegetation. Freshwater Biology, 55(3), 701-715.

Renou-Wilson, F., Moser, G., Fallon, D., Farrell, C. A., Müller, C., & Wilson, D. (2019). Rewetting degraded peatlands for climate and biodiversity benefits: Results from two raised bogs. Ecological Engineering, 127, 547-560.

Riaño Peña, L. C., Guêné-Nanchen, M., Janssen, P., Poulin, M., & Rochefort, L. (2026). Environmental influences on plant diversity in restored and natural peatland pools. Botany 104, 1-26. https://cdnsciencepub.com/doi/10.1139/cjb-2025-0044 .

Riis, T. & Sand-Jensen, K. (2006) Dispersal of plant fragments in small streams. Freshwater Biology, 51, 274–286. https://doi.org/10.1111/j.1365-2427.2005.01496.x

Robroek, B.J.M., Jassey, V.E.J., Kox, M.A.R., Berendsen, R.L., Mills, R.T.E., Cécillon, L., Puissant, J., Meima-Franke, M., Bakker, P.A.H.M., Bodelier, P.L.E., 2015. Peatland vascular plant functional types affect methane

dynamics by altering microbial community structure. Journal of Ecology 103, 925–934. https://doi.org/10.1111/1365-2745.12413

Rochefort, L. (2000) Sphagnum - A keystone genus in habitat restoration. Bryologist, 103, 503–508. https://doi.org/10.1639/0007-2745(2000)103[0503:SAKGIH]2.0.CO;2

Rochefort, L., LeBlanc, M. C., Bérubé, V., Hugron, S., Boudreau, S., & Pouliot, R. (2016). Reintroduction of fen plant communities on a degraded minerotrophic peatland. Botany, 94(11), 1041-1051.

Rochefort, L., Quinty, F., Campeau, S., Johnson, K. & Malterer, T. (2003) North American approach to the restoration of Sphagnum dominated peatlands. Wetlands Ecology and Management, 11(1-2), 3–20, https://doi.org/10.1023/A:1022368805283

Rochefort, L., Strack, M., Chimner, R., (2022). Regional Assessment for North America, in: Global Peatlands Assessment–The State of the World's Peatlands: Evidence for Action Towards Conservation, Restoration and Sustainable Management of Peatlands. United Nations Environment Programme, Nairobi, 193–200.

Roznere, I., & Titus, J. E. (2017). Zonation of emergent freshwater macrophytes: responses to small-scale variation in water depth. The Journal of the Torrey Botanical Society, 144(3), 254-266.

Rydin, H., Jeglum, J. K. (2013). The biology of peatlands, 2nd ed. Oxford University Press, Oxford.

Räsänen, A., Albrecht, E., Annala, M., Aro, L., Laine, A.M., Maanavilja, L., Mustajoki, J., Ronkanen, A.K., Silvan, N., Tarvainen, O., & Tolvanen, A. (2023). After-use of peat extraction sites – A systematic review of biodiversity, climate, hydrological and social impacts. Science of the Total Environment, 882, 163583, https://doi.org/10.1016/j.scitotenv.2023.163583

Salonen, V., 1994. Revegetation of harvested peat surfaces in relation to substrate quality. Journal of Vegetation Science 5, 403–408. https://doi.org/10.2307/3235863

Santamaría, L. (2002). Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecologica, 23(3), 137-154.

Sapkota, R. P., Rijal, K., Stahl, P. D., Pyakurel, B., & Gautam, A. P. (2021). Evidences of homogenization in species assemblages of restored mixed Shorea robusta forest stands of Nepal. Global Ecology and Conservation, 27, e01573.

Sarneel, J.M., (2013). The dispersal capacity of vegetative propagules of riparian fen species. Hydrobiologia, 710, 219–225. https://doi.org/10.1007/s10750-012-1022-3

Schwieger, S., Kreyling, J., Couwenberg, J., Smiljanić, M., Weigel, R., Wilmking, M., Blume-Werry, G., (2021). Wetter is Better: Rewetting of Minerotrophic Peatlands Increases Plant Production and Moves Them Towards Carbon Sinks in a Dry Year. Ecosystems 24, 1093–1109. https://doi.org/10.1007/s10021-020-00570-z

Schwintzer, C.R. (1978). Vegetation and nutrient status of northern Michigan fens. Canadian Journal of Botany, 56, 3044–3051. https://doi.org/10.1139/b78-368

Shingala, M.C., Rajyaguru, A., (2015). Comparison of post hoc tests for unequal variance. International Journal of New Technologies in Science and Engineering 2(5), 22-33.

Sirová, D., Adamec, L., Vrba, J., (2003). Enzymatic activities in traps of four aquatic species of the carnivorous genus Utricularia. New Phytologist 159, 669–675. https://doi.org/10.1046/j.1469-8137.2003.00834.x

Sjörs, H. (1959). Bogs and fens in the Hudson Bay Lowlands. Arctic, 12(1), 3-19. https://doi.org/10.14430/arctic3709

Slack, N.G., Vitt, D.H., & Horton, D.G. (1980). Vegetation gradients of minerotrophically rich fens in western Alberta. Canadian Journal of Botany, 58, 330–350. https://doi.org/10.1139/b80-034

Society for Ecological Restoration International (SER). (2004). The SER international primer on ecological restoration. Society for Ecological Restoration International, Tucson. 14 p.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution, 31(1), 67-80.

Solar, R. R. D. C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., Louzada, J., Maués, M., Moura, N. G., Oliveira, V. H. F., Chaul, J. C. M., Schoereder, J. H., Vieira, I. C. G., Mac Nally, R., & Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecology Letters, 18(10), 1108–1118.

Soons, M. B. (2006). Wind dispersal in freshwater wetlands: knowledge for conservation and restoration. Applied Vegetation Science, 9(2), 271-278.

Standen, V., Rees, D., Thomas, C. J.., & Foster, G. N. (1998). The macro-invertebrate fauna of pools in open and forested patterned mires in the Sutherland Flows, north Scotland. Dans: Patterned Mires and Mire Pools: Origin and Development: Flora and Fauna: Proceedings, University of Durham, 6–7 April 1998. Standen, V., Tallis, J. H., & Meade, R. (éd.). British Ecological Society, Londres.

Strack, M., Kellner, E., & Waddington, J. M. (2005). Dynamics of biogenic gas bubbles in peat and their effects on peatland biogeochemistry. Global Biogeochemical Cycles, 19(1).

Strack, M., Waddington, J.M., Bourbonniere, R.A., Buckton, E.L., Shaw, K., Whittington, P. & Price, J.S. (2008) Effect of water table drawdown on peatland dissolved organic carbon export and dynamics. Hydrological Processes, 22(22), 3373–3385. https://doi.org/10.1002/hyp.6931

Stückler, S., Sonnleitner, R., & Schweiger, S. (2024). Water bodies created by peatland restoration are potential habitats for amphibians and reptiles. Herpetozoa, 37, 347-358.

Sundermann, A., Stoll, S., & Haase, P. (2011). River restoration success depends on the species pool of the immediate surroundings. Ecological Applications, 21(6), 1962-1971.

Taillardat, P., Linkhorst, A., Deblois, C. P., Prijac, A., Gandois, L., Tremblay, A., & Garneau, M. (2024). A carbon source in a carbon sink: Carbon dioxide and methane dynamics in open-water peatland pools. Global Biogeochemical Cycles, 38(4), e2023GB007909.

Tanneberger, F., Moen, A., Barthelmes, A., Lewis, E., Miles, L., Sirin, A., Joosten, H., & Succow, M. (2021). Mires in Europe—Regional diversity, condition and protection. Diversity, 13(8), 381.

Tarnocai, C. (2000). Carbon pools in soils of the Arctic, subarctic, and boreal regions of Canada. In Kimble, J.M. (ed.) Global climate change and cold regions ecosystems. Boca Raton: CRC Press, 103–116.

Timmermann, T., Margóczi, K., Takács, G., & Vegelin, K. (2006). Restoration of peat-forming vegetation by rewetting species-poor fen grasslands. Applied Vegetation Science, 9(2), 241–250. https://doi.org/10.1111/j.1654-109X.2006.tb00673.x

Tischew, S., Baasch, A., Grunert, H. and Kirmer, A. (2014). How to develop native plant communities in heavily altered ecosystems: examples from large-scale surface mining in Germany. Applied Vegetation Science, 17(2), 288–301.

Tomassen, H.B.M., Smolders, A.J.P., Limpens, J., Lamers, L.P.M. & Roelofs, J.G.M. (2004) Expansion of invasive species on ombrotrophic bogs: Desiccation or high N deposition? Journal of Applied Ecology, 41(1), 139–150. https://doi.org/10.1111/j.1365-2664.2004.00870.x

Trowbridge, W.B., 2007. The role of stochasticity and priority effects in floodplain restoration. Ecological Applications 17, 1312–1324. https://doi.org/10.1890/06-1242.1

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. Journal of Geophysical Research: Biogeosciences, 113(G3).

Turetsky, M.R., 2003. The role of bryophytes in carbon and nitrogen cycling. The Bryologist 106(3), 395-409.

Turmel-Courchesne, L., 2019. Remouillage d'un grand fen continental après extraction de tourbe horticole : impacts sur les échanges de carbone et la végétation. M.Sc. thesis, Université Laval, Québec, Québec.

Turmel-Courchesne, L., Davies, M. A., Guêné-Nanchen, M., Strack, M., & Rochefort, L. (2023). Rewetting increases vegetation cover and net growing season carbon uptake under fen conditions after peat-extraction in Manitoba, Canada. Scientific Reports, 13(1), 20588. https://doi.org/10.1038/s41598-023-47879-y

Turner, T.E., Billett, M.F., Baird, A.J., Chapman, P.J., Dinsmore, K.J. & Holden, J. (2016) Regional variation in the biogeochemical and physical characteristics of natural peatland pools. Science of the Total Environment, 545–546, 84–94. https://doi.org/10.1016/j.scitotenv.2015.12.101

Tuukkanen, T., Marttila, H., & Kløve, B. (2014). Effect of soil properties on peat erosion and suspended sediment delivery in drained peatlands. Water Resources Research, 50(4), 3523-3535.

UNEP (2022). Global Peatlands Assessment – The State of the World's Peatlands: Evidence for action toward the conservation, restoration, and sustainable management of peatlands. Main Report. Global Peatlands Initiative. United Nations Environment Programme, Nairobi.

van Breemen, N. (1995) How Sphagnum bogs down other plants. Trends in Ecology & Evolution, 10, 270–275. https://doi.org/10.1016/0169-5347(95)90007-1

van der Wal, R., Pearce, I.S.K. & Brooker, R.W. (2005) Mosses and the struggle for light in a nitrogen-polluted world. Oecologia, 142(1), 159–168. https://doi.org/10.1007/s00442-004-1706-0

Vanschoenwinkel, B., Hulsmans, A.N.N., De Roeck, E.L.S., De Vries, C., Seaman, M. and Brendonck, L. (2009). Community structure in temporary freshwater pools: disentangling the effects of habitat size and hydroregime. Freshwater Biology, 54(7), 1487–1500.

Verberk, W. C. E. P., van Duinen, G. A., Brock, A. M. T., Leuven, R. S. E. W., Siepel, H., Verdonschot, P. F. M., van der Velde, G., & Esselink, H. (2006). Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. Journal for Nature Conservation, 14(2), 78–90. https://doi.org/10.1016/j.jnc.2005.11.002.

Verhoeven, J. T. A., Maltby, E., & Schmitz, M. B. (1990). Nitrogen and Phosphorus Mineralization in Fens and Bogs. Journal of Ecology, 78(3), 713–726. https://doi.org/10.2307/2260894

Vitt, D. H. (2006). Functional characteristics and indicators of boreal peatlands. P. 9-24 dans : Boreal peatland ecosystems. Wieder, R.K., & Vitt, D.H. (éd.). Ecological Studies, vol 188. Springer, Berlin, Heidelberg .

Vitt, D. H., Li, Y., & Belland, R. J. (1995). Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist, 218-227.

Vitt, D.H. (1994). An overview of factors that influence the development of Canadian peatlands. The Memoirs of the Entomological Society of Canada, 126(S169), 7–20.

Vitt, D.H. (2014) A key and review of bryophytes common in North American peatlands. Evansia, 31, 121–158. https://doi.org/10.1639/079.031.0402

Vitt, D.H., 2006. Functional characteristics and indicators of boreal peatlands. Pp. 9-24 in: Boreal peatland ecosystems. Wieder, R.K., Vitt, D.H. (eds.), Ecological Studies 188, Springer, Berlin.

Vitt, D. H., & House, M. (2021). Bryophytes as key indicators of ecosystem function and structure of northern peatlands. *Bryophyte Diversity and Evolution*, *43*(1), 253-264.

Vitt, D.H., House, & M., Glaeser, L. (2022). The response of vegetation to chemical and hydrological gradients at a patterned rich fen in northern Alberta, Canada. Journal of Hydrology: Regional Studies, 40, 101038. https://doi.org/10.1016/j.ejrh.2022.101038

Vitt, D.H., House, M. and Glaeser, L.C. (2024). Regional variation in the distribution of patterned fens in the montane-boreal regions of Alberta, Canada. Wetlands Ecology and Management, 32(3), 367–380.

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., & Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. Ecohydrology, 8(1), 113-127.

Walker, D., & Walker, P. M. (1961). Stratigraphic evidence of regeneration in some Irish bogs. Journal of Ecology, 169-185.

Wang, L., Zhang, H., Tao, Y., Zhang, T., Li, X., Yu, X., ... & Gao, Y. (2025). Fluctuating saline conditions favor competition of Bolboschoenus planiculmis, a dominant species in inland salt marshes. Ecological Processes, 14(1), 67.

Wang, M., Tian, J., Bu, Z., Lamit, L. J., Chen, H., Zhu, Q., & Peng, C. (2019). Structural and functional differentiation of the microbial community in the surface and subsurface peat of two minerotrophic fens in China. Plant and Soil, 437(1), 21-40.

Ward, S. E., Bardgett, R. D., McNamara, N. P., & Ostle, N. J. (2009). Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. Functional Ecology, 23(2), 454–462. https://doi.org/10.1111/j.1365-2435.2008.01521.x

Warner, B.G. (2005). Canadian peatlands. Mires, from Siberia to Tierra del Fuego. In: Mires from Siberia to Tierra del Fuego. G. Steiner (ed.), Landesmuseen, Vienna. Neue Serie 35 pp. 353-372.

Warner, B.G. and Asada, T. (2006). Biological diversity of peatlands in Canada. Aquatic Sciences, 68(3), 240–253.

Wassen, M. J., Peeters, W. H., & Olde Venterink, H. (2003). Patterns in vegetation, hydrology, and nutrient availability in an undisturbed river floodplain in Poland. Plant Ecology, 165(1), 27-43.

Watmough, S., Gilbert-Parkes, S., Basiliko, N., Lamit, L.J., Lilleskov, E.A., Andersen, R., del Aguila-Pasquel, J., Artz, R.E., Benscoter, B.W., Borken, W., Bragazza, L., Brandt, S.M., Bräuer, S.L., Carson, M.A., Chen, X., Chimner, R.A., Clarkson, B.R., Cobb, A.R., Enriquez, A.S., Farmer, J., Grover, S.P., Harvey, C.F., Harris, L.I., Hazard, C., Hoyt, A.M., Hribljan, J., Jauhiainen, J., Juutinen, S., Kane, E.S., Knorr, K.-H., Kolka, R., Könönen, M., Laine, A.M., Larmola, T., Levasseur, P.A., McCalley, C.K., McLaughlin, J., Moore, T.R., Mykytczuk, N., Normand, A.E., Rich, V., Robinson, B., Rupp, D.L., Rutherford, J., Schadt, C.W., Smith, D.S., Spiers, G., Tedersoo, L., Thu, P.Q., Trettin, C.C., Tuittila, E.-S., Turetsky, M., Urbanová, Z., Varner, R.K., Waldrop, M.P., Wang, M., Wang, Z., Warren, M., Wiedermann, M.M., Williams, S.T., Yavitt, J.B., Yu, Z.-G., Zahn, G. (2022) Variation in carbon and nitrogen concentrations among peatland categories at the global scale. PLOS One, 17, e0275149. https://doi.org/10.1371/journal.pone.0275149

Wells, E. Doyle. (1996) Classification of peatland vegetation in Atlantic Canada. Journal of Vegetation Science 7(6), 847-878.

Wheeler, B. D., & Proctor, M. C. F. (2000). Ecological gradients, subdivisions and terminology of north-west European mires. Journal of Ecology: Essay Reviews, 88(2), 187-203.

Whitehouse, H. E., & Bayley, S. E. (2005). Vegetation patterns and biodiversity of peatland plant communities surrounding mid-boreal wetland ponds in Alberta, Canada. Canadian Journal of Botany, 83(6), 621-637.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. Taxon, 21(2-3), 213-251.

Whittington, P. N., & Price, J. S. (2006). The effects of water table draw-down (as a surrogate for climate change) on the hydrology of a fen peatland, Canada. Hydrological Processes, 20(17), 3589-3600.

Wilcox, D.A., Buckler, K. and Czayka, A. (2018). Controlling cattail invasion in sedge/grass meadows. Wetlands, 38(2), 337–347.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., & Sear, D. (2004). Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biological Conservation, 115(2), 329-341.

Wojciechowski, A. A., Blair, J. M., Collins, S. L., & Baer, S. G. (2024). Heterogeneity promotes resilience in restored prairie: Implications for the environmental heterogeneity hypothesis. Ecological Applications, 34(6), e3006.

Wortley, L., Hero, J. M., & Howes, M. (2013). Evaluating ecological restoration success: a review of the literature. Restoration Ecology, 21(5), 537-543.

Xu, J., Morris, P. J., Liu, J., & Holden, J. (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. Catena, 160, 134-140.

Xu, X., Zhang, Q., Tan, Z., Li, Y., & Wang, X. (2015). Effects of water-table depth and soil moisture on plant biomass, diversity, and distribution at a seasonally flooded wetland of Poyang Lake, China. Chinese Geographical Science, 25(6), 739-756.

Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: a review. Biogeosciences, 9(10), 4071-4085.

Zobel, M., van der Maarel, E. and Dupré, C. (1998). Species pool: the concept, its determination and significance for community restoration. Applied Vegetation Science, 1(1), 55–66.

Zoltai, S.C. & Vitt, D.H. (1995) Canadian wetlands: Environmental gradients and classification. Vegetatio, 118, 131–137. https://doi.org/10.1007/BF00045195

Zoltai, S.C. (1987) Peatlands and marshes in the wetland regions of Canada. Memoirs of the Entomological Society of Canada, 119, 5–13. https://doi.org/10.4039/entm119140005-1

Šebelíková, L., Řehounková, K. and Prach, K. (2016). Spontaneous revegetation vs. forestry reclamation in post-mining sand pits. Environmental Science and Pollution Research, 23(14), 13598–13605.