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DRIVERS OF ZOOPLANKTON STRUCTURE AND FUNCTION OVER LARGE SPATIAL AND TEMPORAL SCALES ACROSS CANADA

THESIS

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CINDY PAQUETTE

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FACTEURS AFFECTANT LA STRUCTURE ET LA FONCTION DES COMMUNAUTÉS DE ZOOPLANCTON SOUS UNE LARGE ÉCHELLE SPATIALE ET TEMPORELLE À TRAVERS LE CANADA

THÈSE

PRÉSENTÉE

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AVANT-PROPOS

Les chapitres de cette présente thèse ont été rédigés sous format d'articles scientifiques scientifiques, en anglais. Je suis la première auteure des trois chapitres. J'ai été responsable de la rédaction des manuscrit, de l'acquisition et de l'analyse des données. Mes superviseures de recherche, Beatrix Beisner et Irene Gregory-Eaves, ont contribué substantiellement à la conception, à l'interprétation et à la rédaction des manuscrits de l'étude. Katherine Griffiths a contribué à l'analyse et à l'interprétation des données du troisième chapitre.

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ADN	Acide désoxyribonucléique
ANOVA	Analysis of variance
B-filtration	*Bosmina*-filtration
Bi	Bismuth
C-filtration	*Chydorus*-filtration
Ca	Calcium
CAP	Canonical analysis of principal coordinates
Chl*a*	chlorophyll-*a*
Cl	Chloride
CVRE	cross-validation error
D-filtration	*Daphnia*-filtration
DIC	Dissolved inorganic carbon
DO	dissolved oxygen
DOC	Dissolved organic carbon
FDis	Functional dispersion
FEve	Functional wvenness
FRic	Functional richness
GAMM	Generalized additive mixed model
K	Potassium
LakePulse	*NSERC Canadian Lake Pulse Network*
LCBD	Local contribution to β-diversity
MANOVA	multivariate analysis of variance
maxTL	Maximum trophic level
Na	Sodium
Pb	Lead
PCA	Principal component analysis
PCoA	Principal coordinate analysis

pH	Potential of hydrogen
R^2	R-Squared: coefficient of determination
R^2_{adj}	Adjusted R-Squared
RDA	Redundancy analyses
RF	random forest
S-filtration	*Sidae*-filtration
SCBD	Species contribution to β-diversity
SRP	Soluble reactive phosphoru
TBI	Temporal β-diversity Indices
TN	Total nitrogen
TP	Total phosphorus
URT	Univariate regression trees
VIF	variation inflation factor
α-diversity	Alpha (local) diversity
β-diversity	Beta diversity (spatial or temporal turnover)

LISTE DES SYMBOLES ET DES UNITÉS

< – Plus petit

> – Plus grand

g – Gramme

Km – Kilometer

L – Litter

m – Meter

ml – Milliliter

mm – Millimiter

p – p-value

µ – Micro

RÉSUMÉ

Le Canada contient plus d'un million de lacs, lesquels apportent de nombreux services écosystémiques aux résidents. L'eau potable, les activités récréotouristiques et la pêche sont tous des services offerts par ces écosystèmes qui font partie intégrante de la culture canadienne et de ses activités sociales et économiques. Les activités humaines peuvent toutefois influencer et menacer les ressources en eaux douces et altérer les services écosystémiques offerts par les lacs. Entre autres, l'agriculture intensive, l'industrialisation, l'urbanisation et les changements climatiques sont tous des vecteurs menant à la perturbation des environnements lacustres. De plus, les connaissances scientifiques concernant l'état de santé des lacs canadiens et l'impact des perturbations anthropiques sont limitées et fragmentées. Dans un contexte de conservation de la biodiversité et de gestion pérenne des services écosystémiques, il est donc pressant d'avoir un portrait détaillé des conditions actuelles et passées des lacs. Cette thèse de doctorat prend place dans le réseau du CRSNG sur l'état des lacs du Canada (LakePulse; *NSERC Canadian Lake Pulse Network*). Le but de ce projet pancanadien est d'évaluer l'état de santé des lacs canadiens, de déterminer comment ceux-ci ont changé durant l'ère géologique moderne (l'Anthropocène) et de prédire comment ils continueront d'évoluer dans le futur. Pour ce faire, 664 lacs ont été échantillonnés à travers 12 écozones canadiennes, considérant un gradient de taille de lacs et d'impact humain. Plus d'une centaine de variables ont été examinées dans chacun des lacs, incluant de nombreux paramètres physiques, chimiques et taxonomiques permettant de caractériser la qualité de l'eau.

Étant donné sa position centrale dans la chaine alimentaire aquatique, ainsi que la préservation de certains groupes dans les sédiments des lacs, le zooplancton est un excellent bio-indicateur de la qualité de l'eau. Les traits fonctionnels caractérisant le zooplancton peuvent également être directement liés à différentes fonctions écosystémiques. L'objectif principal de la présente thèse était donc d'explorer les moteurs de changements de la structure de la communauté et des traits fonctionnels du zooplancton sous une large échelle spatiale et temporelle. Plus précisément, dans le premier chapitre, nous avons examiné les variations de composition et de diversité du zooplancton à travers le Canada, tout en explorant les gradients géographiques ainsi que les mécanismes déterminant la distribution du zooplancton. Cette étude nous a permis d'observer que les patrons biogéographiques de la composition et de la diversité du zooplancton étaient structurés par les délimitations des bassins hydrographiques continentaux. Nous avons également établi que la biogéographie du zooplancton canadien était régie par d'importantes barrières physiques à la dispersion, combiné à l'effet structurant des changements climatiques créant un fort gradient longitudinal en composition et en diversité. Dans le deuxième chapitre, ces patrons spatiaux ont été reliés aux variables environnementales caractérisant les lacs pour déterminer comment la diversité et la composition du zooplancton étaient influencées par la qualité de l'eau, la morphométrie des lacs, l'utilisation du sol et la prédation par le poisson. Nos résultats ont démontré que les variables morphométriques étaient les plus importantes pour prédire la diversité du zooplancton, alors que les variables de qualité d'eau étaient davantage importantes pour structurer la composition des communautés. Nous avons également observé une forte hétérogénéité spatiale à travers le Canada, avec des effets divergents des facteurs environnementaux entre les bassins hydrographiques continentaux. Finalement, nous avons utilisé le zooplancton cladocère subfossile préservé dans les sédiments pour déterminer où, et comment, les lacs canadiens ont changé durant l'Anthropocène en relation avec l'utilisation du sol. Cette étude nous a permis de confirmer que les assemblages de cladocères contemporains étaient moins diversifiés que par le passé, et que les communautés étaient structurées par le degré et le type d'utilisation du sol à l'échelle du bassin versant.

Globalement, les résultats de cette première étude uniforme combinant la taxonomie et les traits fonctionnels du zooplancton à travers le Canada nous ont permis d'établir l'importance du zooplancton comme indicateur de changement et de santé des écosystèmes lacustres. Nous avons en effet relevé d'importants patrons biogéographiques dans les communautés de zooplancton, une forte réponse aux variables environnementales, ainsi qu'un changement temporel en relation aux activités humaines. Cette étude nous permet donc de mieux comprendre l'état de santé des lacs canadiens en général, ainsi que les conséquences des activités humaines sur le zooplancton.

Mots clés : Biogéographie, Bassins continentaux, Structure des communautés, Patrons à large échelle spatiale, Zooplancton, Paléolimnologie, Traits fonctionnels

ABSTRACT

Canada contains more than one million lakes, which provide many ecosystem services to residents. Drinking water, recreational tourism and fishing are all services provided by these ecosystems that are an integral part of Canadian culture and its social and economic activities. However, human activities can influence and threaten freshwater resources and alter the ecosystem services provided by lakes. Among others, intensive agriculture, industrialization, urbanization and climate change are all vectors leading to the disturbance of lake ecosystems. In addition, scientific knowledge regarding the health of Canadian lakes and the impacts of anthropogenic disturbances is limited and fragmented. In a context of biodiversity conservation and sustainable management of ecosystem services, it is therefore urgent to have a detailed portrait of the current and past lake condition. This doctoral thesis takes place in NSERC Canadian Lake Pulse Network. The goal of this pan-Canadian project is to assess the health of Canadian lakes, to determine how they have changed during the modern geological era (the Anthropocene) and to predict how they will continue to change in the future. To do this, 664 lakes were sampled across 12 Canadian ecozones, considering a gradient of lake size and human impact. More than a hundred variables were examined in each of the lakes, including numerous physical, chemical and taxonomic parameters used to characterize water quality.

Given its central position in the aquatic foodweb, as well as the preservation of certain groups in lake sediments, zooplankton is an excellent bio-indicator of water quality. The functional traits characterizing zooplankton can also be directly linked to different ecosystem functions. The main objective of this thesis was therefore to explore the drivers of changes in the community structure and functional traits of zooplankton on a large spatial and temporal scale. More specifically, in the first chapter, we examined variations in the composition and diversity of zooplankton across Canada, while exploring the geographic gradients as well as the mechanisms determining the distribution of zooplankton. This study allowed us to observe that the biogeographical patterns of the composition and diversity of zooplankton were structured by the delimitations of the continental hydrographic basins. We also established that the biogeography of Canadian zooplankton was governed by significant physical barriers to dispersal, combined with the structuring effect of climate change, creating a strong longitudinal gradient in composition and diversity. In the second chapter, these spatial patterns were linked to environmental variables characterizing the lakes to determine how the diversity and composition of zooplankton were influenced by water quality, lake morphometry, land use and fish predation. Our results demonstrated that morphometric variables were the most important in predicting zooplankton diversity, while water quality variables were more important in structuring community composition. We also observed strong spatial heterogeneity across Canada, with divergent effects of environmental factors between continental watersheds. Finally, we used subfossil cladoceran zooplankton preserved in sediments to determine where, and how Canadian lakes have changed during the Anthropocene in relation to land use. This study allowed us to confirm that contemporary cladoceran assemblages were less diverse than in the past, and that communities were structured by the degree and type of land use at the watershed scale.

Overall, the results of this first uniform study combining zooplankton taxonomic and functional traits dimensions across Canada have allowed us to establish the importance of zooplankton as an indicator of ecosystem change and lake health. Important biogeographical patterns were indeed noted in zooplankton communities, including a strong response to environmental variables, as well as a temporal change in relation to human activities. This study therefore allows us to better understand the health of Canadian lakes in general, as well as the consequences of human activities on lake zooplankton.

Keywords : Biogeography, Continental divide, Canada, Community structure, Large-scale

patterns, Zooplankton, Paleolimnology, Functional traits

INTRODUCTION

Étant donné qu'ils accumulent le ruissellement de bassins versants entiers et qu’ils intègrent et reflètent les changements du paysage, les lacs peuvent être considérés comme des sentinelles de changement. L'eau douce est utilisée dans l'agriculture, la pêche, les loisirs, le tourisme et d'autres activités sociales et économiques. Les écosystèmes d'eau douce sont également des hauts lieux pour la biodiversité par rapport aux systèmes terrestres (Strayer et Dudgeon, 2010). Or, les sources mondiales d'eau douce sont modifiées par l'utilisation des terres et les changements climatiques. Il devient donc de plus en plus urgent de lier les changements dans les lacs aux différents facteurs de stress auxquels ils font face. Cependant, la recherche limnologique n'est souvent pas suffisamment collaborative pour permettre un portrait global des impacts des différents stresseurs lacustres et déterminer les meilleurs indicateurs de la qualité de l'eau.

Avec ses 879 800 lacs de plus de 0,1 km^2 (Messager *et al.*, 2016), le Canada possède la plus grande quantité et la plus grande superficie de lacs de tous les pays du monde. Pour répondre au besoin criant d’établir l’état de santé des lacs canadiens, le réseau LakePulse a bâti un ensemble de données collaboratives couvrant 664 lacs pour comprendre où, comment et pourquoi les lacs canadiens ont changé durant l’Anthropocène (Figure 0.1). Un deuxième objectif du réseau LakePulse était de déterminer comment les communautés aquatiques ont changé avec la perturbation des lacs, et lesquelles peuvent être utilisées comme indicateurs de la santé des lacs canadiens. Ces signaux d'alerte hâtifs permettant de détecter les premiers signes de changement dans un lac sont indispensables, pour pouvoir agir avant que les fonctions écologiques des lacs ne changent, ou que les services écosystémiques qu’ils offrent ne soient menacés. En tant qu’intermédiaire entre la production primaire et les consommateurs secondaires, le zooplancton est un excellent indicateur de la santé du réseau trophique aquatique. Effectivement, la distribution des espèces de zooplancton et la structure des communautés peuvent non seulement être de bons indicateurs de changement dans les lacs, mais sont aussi idéales pour les évaluations à grande échelle spatiale (Griffiths *et al.*, 2019; Pinel-Alloul *et al.*, 2013).

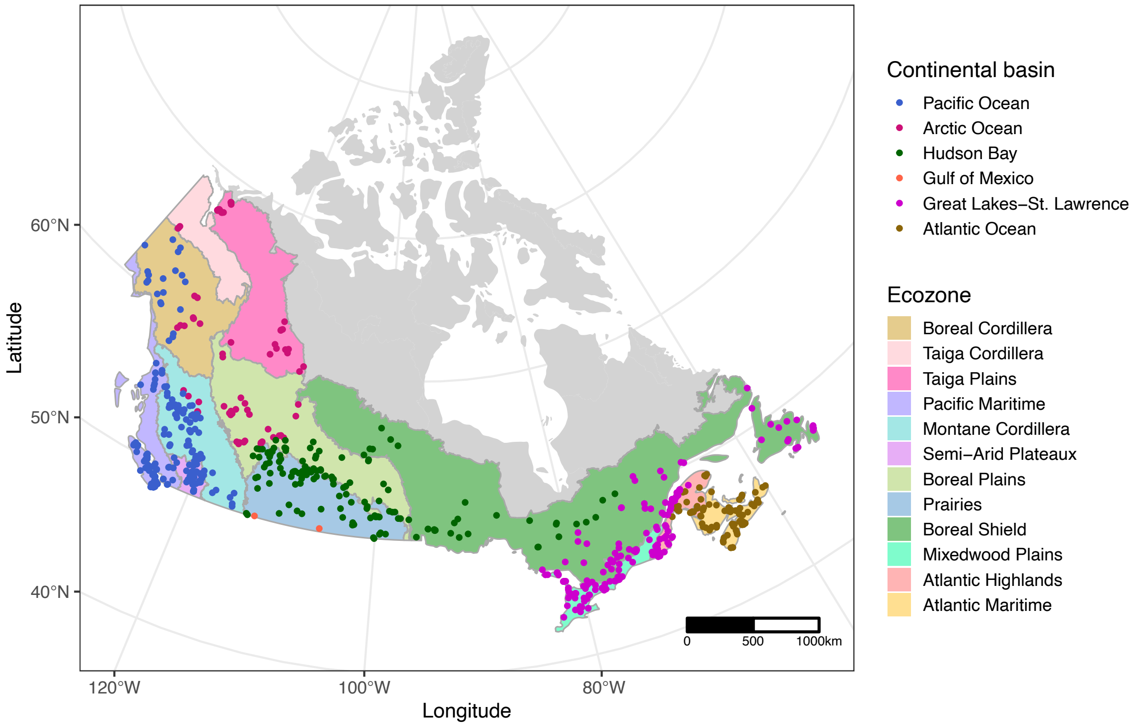

Figure 0.1 Carte des 664 lacs échantillonnés à travers le Canada dans le cadre du réseau LakePulse. Ces lacs se retrouvent dans 12 écozones et 6 bassins versants continentaux. Les régions sont classées d'ouest en est. La carte a été créée avec de la projection Atlas Lambert du Canada (NAD83 SCRS).

0.1 Écozones et basins continentaux

Le territoire du Canada est divisé en 18 écozones terrestres, en fonction des reliefs, du sol, des caractéristiques de l'eau, de la végétation, du climat et des activités humaines (Wiken, 1986). Parmi ces écozones, 12 ont été couvertes par l'échantillonnage LakePulse (Figure 0.1). Ces divisions terrestres peuvent avoir un grand impact initial sur les communautés et la diversité aquatique. Par exemple, les lacs des prairies et des plaines boréales sont parmi les plus riches en éléments nutritifs, avec de faibles rapports azote : phosphore et des proliférations de cyanobactéries toxiques (Haertel, 1976; Hammer, 1971; Quinlan *et al.*, 2002; Taranu *et al.*, 2010), en raison de l'agriculture intensive de ces régions et/ou des dépôts géologiques naturels. Sur le bouclier boréal, il y a une importante activité forestière et une acidification liée aux déclins de phosphore et de calcium dans les lacs (Jeziorski *et al.*, 2008; Yan, Paterson, *et al.*, 2008; Yan, Somers, *et al.*, 2008). En général, les régions du sud du Canada sont fortement touchées par l'agriculture et l'urbanisation, y compris certaines parties du bouclier boréal, des plaines à forêt mixtes et des maritimes de l’Atlantique. Une description détaillée des principales activités humaines dans chacune des écozones du Canada est présentée au tableau 0.1.

Tableau 0.1 Principaux axes des impacts anthropiques dans chacune des écozones étudiées du Canada, selon Wiken (1986), Brown et Lomolino (1998) and Gibbs et al., (2009).

Écozone	**Mines**	**Urbanisation**	**Foresterie**	**Pâturage**	**Agriculture**
Cordillère Boréale	x		x		
Maritime du Pacifique		x	x		
Plateaux semi-arides		x			x
Cordillère montagnarde	x		x	x	
Prairies	x			x	x
Plaines Boréales			x	x	x
Plaines à forêt mixtes		x		x	
Maritimes de l’Atlantique			x		x
Hautes terres de l’Atlantique		x	x		x
Bouclier boréal	x		x		
Taïga cordillère	x		x		
Taïga des plaines	x		x		

Le Canada peut également être subdivisé en différents bassins hydrologiques continentaux, lesquels délimitent la surface du paysage où les précipitations et les systèmes fluviaux s'écoulent vers des golfes, mers ou océans distincts. L’échantillonnage du réseau LakePulse a couvert six bassins versants continentaux : l’océan Pacifique, l’océan Arctique, la baie d'Hudson, le golfe du Mexique, les grands Lacs-St. Saint-Laurent et l’océan Atlantique (Figure 0.1). Étant directement reliées aux dynamiques hydriques, ces divisions ont le potentiel d’influencer directement les caractéristiques des lacs et les communautés aquatiques (voir chapitre I pour plus de détails).

0.2 Le zooplancton, sentinelle du changement

Le zooplancton compose le groupe planctonique hétérotrophe qui se nourrit des principaux mobilisateurs d'énergie (phytoplancton et bactéries) des réseaux trophiques lacustres. En tant que consommateurs primaires, le zooplancton est une source alimentaire importante des prédateurs macroinvertébrés et des poissons, et donc un lien trophique critique dans le transfert d'énergie vers le haut de la chaine alimentaire. Les changements dans les communautés de zooplancton peuvent donc être décisifs pour le fonctionnement de l'ensemble de l'écosystème des lacs étant donné leur position centrale dans le réseau trophique, assurant la médiation des transferts d'énergie ascendants et descendants. Le zooplancton est également directement sensible aux impacts anthropiques et peut être un bon indicateur de la qualité de l'eau (Caroni et Irvine, 2010). Par exemple, des changements dans la répartition des espèces de zooplancton ou dans leur diversité peuvent se produire après une perturbation et peuvent être interprétés comme un signe avant-coureur de perturbation de l’écosystème (Patalas *et al.*, 1994).

0.3 Structure de la communauté zooplanctonique

La structure de la communauté implique à la fois la composition des espèces (nombre d'individus dans chaque groupe) et la diversité (une représentation quantitative de la communauté). La structure et la diversité peuvent être estimées à l'aide de groupes taxonomiques, ainsi que de traits fonctionnels, lesquels reflètent la fonction des espèces dans l’écosystème. De plus, la diversité autant taxonomique que fonctionnelle peut être considérée à trois échelles spatiales : alpha, gamma et bêta. La diversité alpha estime la diversité locale, gamma est la somme régionale du nombre d'espèces et la diversité bêta considère les différences de diversité dans l’espace (entre les sites) ou dans le temps.

0.3.1 Approches taxonomiques

L'approche la plus commune pour décrire la structure d’une communauté est l’utilisation de l’abondance ou de la biomasse de taxons. La composition en espèces d’un écosystème peut être directement utilisée pour caractériser une communauté. Des indices de diversité, calculés à partir de ces compositions peuvent par la suite fournir des valeurs sommaires pour décrire la variété des espèces, et comparer différents sites.

Il existe quatre indices couramment utilisés et complémentaires de diversité taxonomique alpha (Hill, 1973). La richesse en espèces est une simple somme du nombre d'espèces sur un site, comme le nombre d'espèces de zooplancton dans un lac. Souvent, la richesse en espèces est raréfiée au nombre total, en corrigeant les différents nombres d'individus comptés sur chaque site. Le deuxième indice est l'équité de Pielou, qui calcule la régularité de la biomasse ou du nombre d'individus répartis entre les espèces d'un site. Si toutes les espèces sont présentes à la même densité, une communauté a une équité maximale, tandis que des valeurs faibles d'équité indiquent qu'une ou quelques espèces sont fortement dominantes. L'entropie de Shannon est un indice qui intègre la richesse en espèces à l'équité, étant maximal à une équité maximale et à une richesse élevée. Finalement, l'index de Simpson considère l'abondance seule des espèces les plus abondantes d'un site, et reflète donc la dominance de certains groupes.

La diversité bêta spatiale taxonomique permet la comparaison de la composition des espèces entre les sites ou les régions (Whittaker, 1972) et a été un outil essentiel dans la conservation et la gestion de la biodiversité (Legendre *et al.*, 2005), car elle permet d'identifier les espèces ou les sites critiques pour le maintien de la diversité régionale. Parce que les changements de composition sont plus fréquents que les changements de richesse au cours de l'Anthropocène (Dornelas *et al.*, 2014; Vellend *et al.*, 2013), la diversité bêta est un outil clé pour souligner les patrons importants de biodiversité qui demeurent non détectés à l'aide d'autres indices de diversité alpha (Winegardner *et al.*, 2017). La diversité bêta peut également être analysée d'un point de vue temporel, en comparant les communautés d'un même site sous deux échelles temporelles distinctes (Legendre, 2019). Cette approche permet de comparer le degré de changement temporel dans la composition de différentes communautés. En effet, il existe une différence importante entre la perte d'espèces et la perte de diversité. Selon des études et des méta-analyses récentes, la richesse spécifique temporelle a été plus ou moins stable localement (et régionalement) au cours des derniers siècles (e.g. Dornelas *et al.*, 2014; Vellend *et al.*, 2013). Contrairement à la richesse spécifique, la composition de la communauté varie considérablement avec la perte et l'invasion d'espèces locales (Dornelas *et al.*, 2014; Newbold *et al.*, 2015; Vellend *et al.*, 2013). La diversité bêta temporelle nous permet donc d'examiner l'effet net de ces changements de composition.

0.3.2 Approches fonctionnelles

Alors qu'elles décrivent efficacement les espèces présentes dans un écosystème, les approches taxonomiques ne considèrent pas la façon dont ces espèces interagissent entre elles et avec leur environnement, ni la manière dont elles peuvent en influencer le fonctionnement. L'utilisation des traits fonctionnels permet d'intégrer ces interactions, et d'évaluer le rôle qu'occupe une espèce dans son environnement. Au cours de la dernière décennie, il a été de plus en plus reconnu qu'une approche par traits fonctionnels peut donner des réponses robustes, prévisibles et généralisables à plusieurs questions écologiques (Barton *et al.*, 2013; Litchman *et al.*, 2013; McGill *et al.*, 2006).

Chez le zooplancton, une forte redondance des traits fonctionnels peut être observée entre les espèces (Barnett et Beisner, 2007; Hébert *et al.*, 2016). De nombreuses espèces joueront ainsi des rôles similaires dans l'écosystème et ne considérer que la diversité taxonomique sous-estimerait cette redondance. Dans un contexte de gestion et de conservation des lacs, la fonction du zooplancton pourrait donc mieux traduire les changements de réseau trophique en réponse à une perturbation importante de l'environnement. Par exemple, cette approche a été utilisée pour étudier la réponse du zooplancton et du phytoplancton dans un système associée à l'exploitation minière, permettant de démontrer un découplage de ces deux communautés au niveau fonctionnel suivant l'impact minier (St-Gelais *et al.*, 2018).

De manière analogue à la diversité taxonomique, les principaux indices de diversité fonctionnelle représentent la richesse, l'équité et la dispersion des traits. Les indices de diversité fonctionnelle sont souvent estimés dans un espace fonctionnel créé par des axes représentant chaque trait. Pour chaque communauté, la taille de l'espace fonctionnel est estimée à partir du regroupement relatif des traits représentés (Laliberté et Legendre, 2010; Villéger *et al.*, 2008). La richesse fonctionnelle (FRic) représente le volume d'espace fonctionnel occupé, augmentant avec le nombre de traits représentés (Cornwell *et al.*, 2006; Schleuter *et al.*, 2010; Villéger *et al.*, 2008). L'équité fonctionnelle (FEve) (Villéger *et al.*, 2008) quantifie la régularité de la distribution des espèces dans l'espace fonctionnel (Schleuter *et al.*, 2010). Un indice FEve faible indique que quelques types fonctionnels dominent la communauté ou qu'il y a une faible régularité des distances fonctionnelles entre les espèces. Enfin la dispersion fonctionnelle (FDis) est un indice utilisant la distance moyenne de chaque taxon au centroïde de la communauté dans l'espace des traits (Laliberté et Legendre, 2010) avec des valeurs plus élevées reflétant une plus grande diversité fonctionnelle.

Similairement à la diversité bêta taxonomique, il est également possible d'analyser la similarité fonctionnelle bêta des communautés, afin de détecter les changements de traits fonctionnels entre plusieurs communautés dans l'espace (Swenson *et al.*, 2011; Villéger *et al.*, 2013), ou pour les mêmes communautés, à travers le temps (Legendre, 2019). La diversité bêta fonctionnelle peut être calculée en divisant l'espace fonctionnel non partagé entre deux communautés par l'espace fonctionnel total occupé (Villéger *et al.*, 2013).

Dans le cadre de cette thèse, l'utilisation des traits fonctionnels a permis d'avoir une devise commune à travers un large éventail de classifications taxonomiques, afin d'examiner comment les communautés canadiennes de zooplancton des lacs réagissent (traits de réponse) et influencent (traits d'effet) leur environnement et son fonctionnement (Cadotte *et al.*, 2011; Wallenstein et Hall, 2012). Cette thèse est par ailleurs la première évaluation des traits fonctionnels du zooplancton à travers le Canada, ainsi que la première évaluation de la diversité bêta temporelle fonctionnelle du zooplancton.

0.3.3 Approches paléolimnologiques

Le zooplancton lacustre peut être divisé en deux grands groupes taxonomiques : les cladocères et les copépodes. En raison de leurs parties corporelles relativement molles, les copépodes subfossiles ne sont généralement pas détectables dans les sédiments (Rautio *et al.*, 2000). Au contraire, les cladocères ont la particularité d'avoir des exosquelettes qui se préservent dans les sédiments des lacs lorsqu'ils meurent et se déposent au fond de l'eau. Certaines parties de l'exosquelette (carapaces, postabdomens, griffes, mandibules et casques) peuvent être utilisées pour l'identification des espèces subfossilisées (Korhola et Rautio, 2001). Les cladocères ont une grande diversité d'habitats (Korhola et Rautio, 2001) et sont relativement dispersés via divers processus passifs. L'analyse des cladocères préservés dans les carottes de sédiments peut être utilisée pour suivre l'historique des changements dans les lacs et leur bassin versant, fournissant des informations sur les changements climatiques, les réseaux trophiques ou sur la qualité de l'eau (Korhola et Rautio, 2001). Les assemblages de cladocères subfossiles fournissent également un portrait plus intégré que les échantillons pélagiques et permettent ainsi de suivre les modifications de l'habitat (Korhola et Rautio, 2001). En effet, Winegardner *et al.* (2015) ont constaté que la variation expliquée par l'environnement était plus importante dans les sédiments de surface, représentant les dernières années d'accumulation, que dans la colonne d'eau. De même, une forte relation a été observée entre les conclusions déduites des données paléolimnologiques de cladocères sur les dynamiques trophiques et les observations contemporaines de zooplancton pélagique (Manca *et al.*, 2007). Typiquement, si un changement rapide s'est récemment produit dans l'environnement, les assemblages dans les sédiments de surface devraient changer par rapport aux sédiments plus profonds (Chengalath, 1982; Fryer et Forshaw, 1979; Synerholm, 1979). En analysant les sédiments supérieurs et inférieurs d'une carotte de sédiment d'un lac, il est donc possible de comparer les assemblages contemporains aux assemblages préindustriels (avant 1850 CE) avant l'Anthropocène (Smol, 2009).

0.4 Facteurs influençant la structure des communautés de zooplancton

La macroécologie est le domaine d'étude des patrons de diversité à grande échelle (Brown et Maurer, 1989). Déterminer comment les espèces sont réparties entre les régions et identifier les facteurs affectant ces répartitions sont des questions majeures en écologie et en biogéographie (Gaston, 2000; Lomolino *et al.*, 2010). En effet, la répartition des espèces n'est pas aléatoire sur le territoire et chaque espèce possède une niche écologique différente en fonction de sa tolérance ou sa sensibilité spécifique à une variété de milieux aquatiques (Korhola et Rautio, 2001).

0.4.1 Biogéographie et dispersion

En tant qu'organismes aquatiques, la distribution du zooplancton est fortement limitée par la dispersion entre les lacs (Beisner *et al.*, 2006; De Bie *et al.*, 2012; Padial *et al.*, 2014). Le zooplancton semble se disperser aussi bien par les cours d'eau que par voie terrestre (p. ex. vecteurs éoliens ou animaux) via des stades dormants dans des régions comme celle du paysage du sud du Québec (Beisner *et al.*, 2006). De nombreuses hypothèses ont été proposées pour expliquer les modèles de richesse en espèces à travers les régions (Wiens, 2011). La théorie métabolique (Allen *et al.*, 2002; Brown *et al.*, 2004) propose que la diversité des espèces soit contrôlée par la température de l'air. En parallèle, l'hypothèse richesse-énergie (Brown, 1981; Wright, 1983) stipule que le nombre d'espèces pouvant coexister dans un écosystème est déterminé par la quantité d'énergie (p. ex. rayonnement solaire, précipitations) disponible. Cette théorie a été utilisée pour expliquer la distribution régionale du zooplancton crustacé dans 1 665 lacs canadiens échantillonnés sur 30 ans à partir du début des années 1960 (Brown, 1981; Pinel-Alloul *et al.*, 2013; Wright, 1983). Alternativement, l'hypothèse d'hétérogénéité spatiale (synthétisée par Pianka, 1966) suggère que le nombre d'espèces dans une zone est corrélé au degré d'hétérogénéité de l'environnement. Cette hypothèse est soutenue par des études sur la composition du zooplancton où une variété de processus régionaux et locaux agissent ensemble pour créer des gradients spatiaux (Declerck *et al.*, 2011; Pinel-Alloul, 1995; Pinel-Alloul et Ghadouani, 2007). En tant qu'hypothèse fonctionnelle, l'hypothèse du filtrage de niche suggère que les espèces ayant des traits fonctionnels similaires peuvent être regroupées dans des groupes fonctionnels qui devraient se retrouver dans des habitats similaires (Brind'Amour *et al.*, 2011; Tonn *et al.*, 1990; Zobel, 1997).

0.4.2 Variables environnementales

Dans les lacs nord-américains, le plancton a montré d'importants schémas biogéographiques qui peuvent être liés à des gradients environnementaux (Stomp *et al.*, 2011; Vyverman *et al.*, 2007). Diverses études ont également mis en évidence des réponses des communautés de zooplancton à des facteurs de stress dont : l'eutrophisation (Jeppesen *et al.*, 2011), le pH (DeCosta, 1975; Yan et Strus, 1980), la salinité (Amsinck *et al.*, 2005a, 2005b ; Brucet *et al.*, 2009), le niveau d'eau (Kattel *et al.*, 2007; Nevalainen *et al.*, 2011) et les substances toxiques (Cattaneo *et al.*, 1998; Manca et Comoli, 1995). Cependant, la principale préoccupation dans la gestion de la qualité de l'eau mondialement a été les changements dans les macronutriments (par exemple l'azote et le phosphore) des bassins versants des lacs. Cela est particulièrement important dans les régions où l'activité agricole est intense, comme dans l'écozone des Prairies. L'augmentation de la concentration de phosphore total (TP) en particulier, influence la composition, la diversité et la biomasse du zooplancton, en diminuant généralement la richesse spécifique et en augmentant potentiellement la biomasse à des concentrations plus élevées de TP (Barnett et Beisner, 2007; Dodson *et al.*, 2000; Jeppesen *et al.*, 2000).

D'autre part, dans de nombreux lacs forestiers du Bouclier canadien, les concentrations de TP ont diminué au cours des 30 dernières années, ce qui affecte également les communautés de crustacés et de zooplancton via la réduction des concentrations de nourriture (Yan *et al.*, 2008b). Parallèlement, les concentrations de calcium (Ca) ont également diminué au cours des deux dernières décennies (Jeziorski *et al.*, 2008; Keller *et al.*, 2001) en raison de l'exploitation forestière dans les bassins versants, des dépôts acides historiques et de l'augmentation du pH (Jeziorski *et al.*, 2008; Watmough *et al.*, 2003). Compte tenu de l'importance du Ca pour la formation de la carapace du zooplancton, ces déclins ont entraîné des changements importants dans le zooplancton via une mortalité accrue combinée à des taux de croissance et de reproduction réduits (Azan *et al.*, 2015; Azan et Arnott, 2016). Au cours des 10 prochaines années, 37 % des lacs du Centre-Sud de l'Ontario (situés sur le bassin versant du Bouclier canadien) devraient atteindre le seuil de 1,5 mg Ca/L auquel la croissance et la reproduction des daphnies sont affectées (Reid et Watmough, 2016).

Au fil des ans, de nombreuses recherches se sont concentrées sur l'effet des facteurs de stress individuels sur les communautés de zooplancton, médiés par des changements dans la qualité de l'eau (par exemple, les macronutriments, la température ou les produits chimiques). Cependant, les facteurs de stress agissent simultanément dans les lacs, parfois sur de longues périodes. Par exemple, les changements de pH peuvent interagir avec d'autres facteurs tels que la pression de prédation, la couverture de macrophytes et les concentrations de contaminants (Havens et Decosta, 1987; Korhola et Rautio, 2001; Nilssen et Sandoy, 1990; Paterson, 1994; Uimonen-Simola et Tolonen, 1987). Pourtant, les effets interactifs des changements de la qualité de l'eau et du changement climatique ne sont pas bien compris, en particulier dans des conditions naturelles (Hayden *et al.*, 2017; Titeux *et al.*, 2016). Sur la base d'une méta-analyse de plusieurs facteurs de stress dans les systèmes d'eau douce, l'effet combiné des facteurs de stress semble principalement antagoniste, mais il existe une variabilité considérable entre les différentes combinaisons de facteurs de stress (Jackson *et al.*, 2016).

D’autre part, les variables de morphométrie peuvent aussi régir les communautés de zooplancton. Par exemple, il est connu que les gros écosystèmes peuvent soutenir une plus grande richesse en espèces (Gaston, 2000), un concept qui peut également s’appliquer à la taille ou à la profondeur des lacs. Il a d’ailleurs été démontré que la diversité taxonomique et fonctionnelle du zooplancton était plus grande dans les lacs plus profonds au Canada (Patalas, 1971; St-Gelais *et al.*, 2017).

0.4.3 Espace vs environnement

La taille de l’échelle spatiale étudiée peut influencer l’importance de la variation des paramètres environnementaux dans l’écosystème, influençant ainsi les communautés (Borcard *et al.*, 2004; Declerck *et al.*, 2011). De nombreuses études ont donc tenté de comparer l’importance relative de l’environnement et de l’espace sur la composition ou la diversité du zooplancton (e.g. Beisner *et al.*, 2006; St-Gelais *et al.*, 2017; Symons *et al.*, 2014; Viana *et al.*, 2014), sans obtenir de consensus défini. Dans une étude des mares temporaires des zones humides des Hautes Andes, Deckerk *et al.* (2011) ont conclu qu'à petite échelle, les variables environnementales étaient les processus les plus importants dans la structuration des communautés, tandis qu'à plus grande échelle, les variables spatiales et la limitation de la dispersion étaient plus importantes pour générer la diversité.

0.4.4 Utilisation du sol

Au-delà de la prise en compte des propriétés de l'eau dans le lac, il est important de relier les changements dans les communautés lacustres aux activités humaines sur leurs paysages adjacents, car l'utilisation des terres et la qualité de l'eau sont fortement corrélées (e.g. Lee *et al.*, 2009). Par exemple, les activités humaines telles que l'exploitation minière et l'agriculture entraînent généralement une augmentation des concentrations d'azote ou de phosphore dans les lacs et modifient souvent les rapports azote / phosphore. Étant donné que ces modifications peuvent fortement influencer la concentration et la diversité du phytoplancton (Downing et McCauley, 1992; Saros et Anderson, 2015), il peut y avoir des répercussions sur les communautés de zooplancton qui les consomment.

Les changements dans les pratiques agricoles et l'augmentation de l'agriculture industrielle ont également affecté l'état trophique de nombreux lacs, avec des effets marqués sur les communautés de zooplancton. Outre l’eutrophisation, l’agriculture intensive peut affecter les communautés aquatiques via l’utilisation de pesticides. Ces pesticides, y compris les herbicides et les insecticides, sont en effet une préoccupation croissante pour les écosystèmes d'eau douce, avec une variété d'effets sur le zooplancton, comme la modification du sex-ratio ou de la dynamique des populations et la réduction des abondances (revu par Hanazato, 2001; Hasenbein *et al.*, 2016; Relyea, 2009). Les schémas généraux observés en réponse à l'augmentation des pesticides comprennent une augmentation de la richesse et de la diversité des espèces via une augmentation de la biomasse relative des petites espèces de zooplancton. Par contre, une diminution du transfert d'énergie du phytoplancton au zooplancton est également observée, puisque les herbivores plus efficaces tels que *Daphnia* sont perdus (Hanazato, 1994, 1998; Havens et Hanazato, 1993).

0.4.5 Effets « Top-down »

En raison des cascades trophiques, les variations observées dans les communautés de zooplancton peuvent résulter d'influences indirectes de l'environnement sur les communautés de poissons (effet « top-down » ou descendant). Les variations dans la composition de la communauté de poissons sont le plus souvent attribuées à la morphométrie (O’Brien *et al.*, 2004) ou à la profondeur (Jackson et Harvey, 1989) des lacs et peuvent jouer un rôle majeur dans la structuration des communautés de zooplancton (Gliwicz, 2003). Des changements dans la position trophique dominante des poissons dans un lac (planctivore ou piscivore) peuvent également avoir des effets en cascade sur les niveaux trophiques inférieurs (Carpenter *et al.*, 2001). L’importance de ces effets descendants peut être influencée par les changements climatiques, ou interagir avec la productivité des lacs pour affecter la biomasse et la composition du zooplancton (Gyllström *et al.*, 2005; Hayden *et al.*, 2017).

Dans le contexte du réseau Lake Pulse, l'échantillonnage des poissons n'était pas réaliste puisque les lacs devaient chacun être échantillonnés en une seule journée. En revanche, il a été possible d'obtenir des données sur les poissons des ministères provinciaux et territoriaux pour un sous-ensemble de lacs échantillonnés afin de tester les corrélations potentielles entre la prédation par le poisson et les indices de communauté du zooplancton (voir chapitre II).

0.5 Cadre conceptuel de la thèse

Pour comprendre les distributions des espèces, il est possible de se référer aux « règles d'assemblage » (Diamond, 1975; Weiher et Keddy, 2001) qui façonnent une communauté et expliquent pourquoi un ensemble donné d'espèces est présent sur un site spécifique. Il existe quatre catégories hiérarchiques de règles. Premièrement, les événements historiques tels que les phénomènes biogéographiques à grande échelle et les événements de spéciation détermineront le pool d'espèces qui pourrait éventuellement coloniser une niche donnée (Belyea et Lancaster, 1999). Deuxièmement, la limitation de la dispersion garantira que certaines espèces pourront ou non atteindre un site local pour le coloniser en fonction de la connectivité de l'habitat. Troisièmement, les filtres environnementaux limiteront les espèces qui survivront par la mortalité et la sélection naturelle. Enfin, les dynamiques internes des communautés forgeront le pool d'espèces réalisé sur un site donné, généralement via la prédation, la compétition et le mutualisme. Ces règles n'auront pas la même ampleur d'effet dans différents écosystèmes et fonctionnent généralement pour façonner les communautés à différentes échelles (Declerck *et al.*, 2011; Dray *et al.*, 2012).

Les chapitres de cette thèse peuvent être liés aux règles d'assemblage où l'impact humain s'ajoute du fait de son influence directe sur les filtres environnementaux (Figure 0.2). L’objectif du premier chapitre de cette thèse a été d'identifier les régions canadiennes de haute diversité et de quantifier l'importance relative de différentes échelles spatiales pour les communautés lacustres de zooplancton à travers le Canada. Dans le deuxième chapitre, les variables environnementales (incluant la qualité de l’eau, la morphométrie des lacs, l’utilisation du sol et la prédation par les poissons) influençant la composition et la diversité taxonomique et fonctionnelle ont été explorées. Finalement, dans le troisième chapitre, les changements temporels dans les assemblages subfossiles de cladocères ont été reliés aux changements dans l'utilisation du sol depuis l'ère préindustrielle.

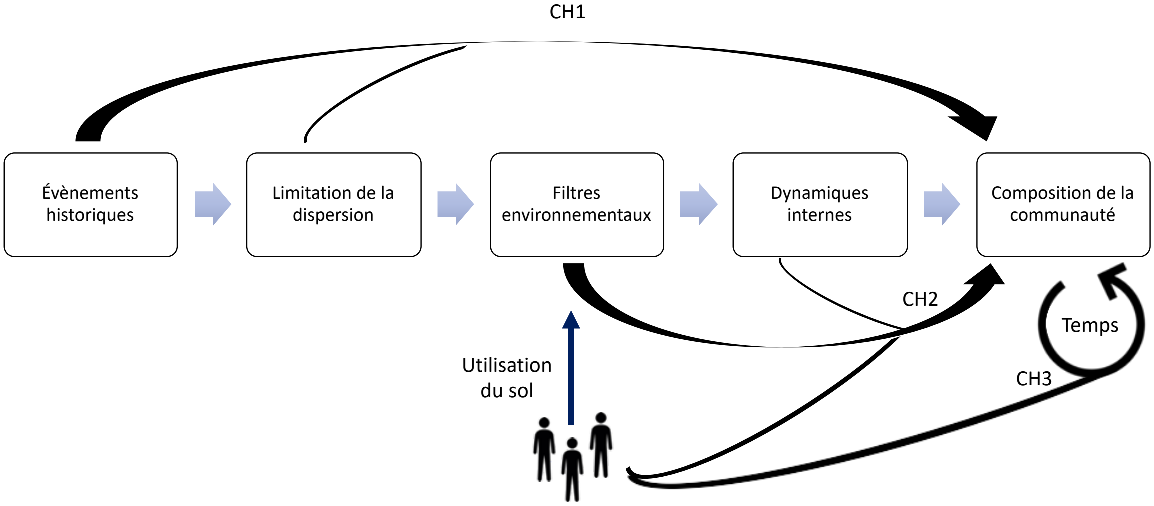

Figure 0.2 Intégration des chapitres selon le cadre des règles d'assemblage, auquel l'utilisation du sol est ajoutée en raison de son influence directe sur les processus de filtrage de l'environnement. Le chapitre I a évalué la biogéographie du zooplancton. Le chapitre II s'est concentré sur les facteurs environnementaux locaux influençant le zooplancton, ainsi que sur l'effet de l'impact humain et de la prédation par le poisson. Enfin, l'évolution des communautés au fil du temps en lien avec les changements d'utilisation du sol a été analysée au chapitre III.

0.6 Approche générale et échantillonnage

0.6.1 Sélection des lacs

Le réseau LakePulse du CRSNG sur l'état des lacs du Canada consiste en une évaluation générale de la santé des lacs canadiens. Sur trois étés, 664 lacs ont été échantillonnés (217 lacs en 2017, 228 en 2018 et 219 lacs en 2019) dans 12 écozones. Les lacs ont été sélectionnés aléatoirement parmi tous les lacs canadiens de ces écozones comprenant un accès routier à moins d'un km selon deux critères: la taille du lac (trois classes de taille : 0,1-1 km^2, 1-10 km^2, 10-100 km^2) et l'impact humain (trois classes d'influence humaine dans le bassin versant, avec des seuils variables entre chaque écozone; voir Huot *et al.,* 2019 pour plus de détails). Un nombre égal de lacs a été aléatoirement sélectionné dans chacune de ces catégories de taille et d'impact humain dans les différentes écozones canadiennes. Dans un ensemble d'écozones principales, un échantillonnage plus étendu a été effectué (bouclier boréal (n=91), maritime de l'Atlantique (n=69), plaines à forêts mixtes (n=65), prairies (n=68), plaines boréales (n=72), cordillère montagnarde (n=69), maritime du Pacifique (n=69), hautes terres de l'Atlantique(n=65) et plateaux semi-arides (n=38)). Dans les écozones secondaires (taïga des plaines (n=25), cordillère boréale (n=30), taïga de la Cordillère (n=3)), l'échantillonnage a eu lieu de façon plus restreinte (Figure 0.1).

0.6.2 Échantillonnage des lacs

Plus de 100 variables biologiques, physiques et chimiques ont été collectées ou mesurées dans chaque lac, incluant l'analyse des caractéristiques de morphométrie des lacs et d'utilisation du sol dans les bassins versants (voir Huot *et al.,* (2019) pour la liste complète des variables échantillonnées ou mesurées). L'échantillonnage a été effectué de façon uniforme dans chaque lacs (NSERC Canadian Lake Pulse Network, 2021), en suivant un protocole élaboré pour s'aligner sur l'évaluation nationale des lacs de l'*Environmental Protection Agency*. Le chapitre II décrit les méthodes d'échantillonnage pour les variables environnementales utilisées dans le contexte de cette thèse. Le zooplancton pélagique a été échantillonné dans 624 lacs (excluant les lacs pour lesquels les critères de comptes n'étaient pas respectés; voir le chapitre I pour une description détaillée de la méthode d'échantillonnage).

Des carottes de sédiments ont également été prélevées au point le plus profond de chacun des lacs, pour offrir un contexte temporel à l'échantillonnage contemporain. Pour le troisième chapitre, un sous-échantillon de 101 lacs des écozones principales a été utilisé pour comparer les assemblages de cladocères subfossiles contemporains et préindustriels. Ces 101 lacs ont été sélectionnées en utilisant le même plan stratifié que pour l'échantillonnage complet, en considérant la taille des lacs et l'impact humain dans les différentes écozones.

0.6.3 Analyses de la structure des communautés

Au fil des trois chapitres de la présente thèse, les communautés de zooplancton ont été analysées à la fois en termes de composition et de diversité, ainsi que sous des approches taxonomiques et fonctionnelles. Pour caractériser la composition taxonomique des communautés, la biomasse a été utilisée. Celle-ci a été calculée en utilisant la longueur moyenne de jusqu'à 10 individus mesurés par taxon par lac, en combinaison avec des relations taille/poids préétablies pour chaque espèce (Dumont *et al*., 1975; McCauley, 1984; Lawrence *et al*., 1987). Les indices de diversité taxonomique utilisés ont été la richesse totale et raréfiée, l'équité, ainsi que les indices de diversité de Shannon et de Simpson.

Les traits fonctionnels utilisés pour caractériser la communauté ont été prélevés de la littérature (Barnett *et al.*, 2007; Griffiths *et al.*, 2019; Hébert *et al.*, 2016; Longhi et Beisner, 2010) et reflètent l'interaction du zooplancton avec son environnement. Des traits liés à l'acquisition des ressources, à l'habitat, à la taille et à la prédation ont été sélectionnés, afin de caractériser les relations dans les réseaux trophiques des lacs. L'acquisition des ressources a été représentée par la stratégie d'alimentation : B(*Bosmina*)-filtration, C(*Chydorus*)-filtration, D(*Daphnia*)-filtration, S(*Sidae*)-filtration, Suspension stationnaire, rapace. Le trait de l'habitat a permis de diviser les espèces selon leur préférence de niche écologique (pélagique, littoral, ou intermédiaire). La position trophique a caractérisé les espèces comme carnivores, omnivores, herbivores, ou une combinaison de ces catégories, selon les préférences alimentaires connues. Finalement, la taille qui est un trait intégrateur important pouvant être influencé par la prédation et l'acquisition de ressources (Litchman *et al.*, 2013), a été estimée à l'aide de la biomasse individuelle moyenne de chaque taxon.

Pour calculer la composition fonctionnelle des assemblages zooplanctoniques (pélagiques et subfossiles), une approche basée sur la biomasse a été utilisée. La biomasse du nombre total d'individus possédant un trait spécifique a d'abord été calculée, puis ce nombre a été divisé par la biomasse totale de la communauté, dans le but d'obtenir la présence relative de chaque trait fonctionnel. Pour estimer la diversité fonctionnelle, nous avons utilisé l'équité fonctionnelle (FEve; Villéger *et al.*, 2008), la richesse fonctionnelle (FRic; Villéger *et al.*, 2008) et la dispersion fonctionnelle (FDis; Laliberté et Legendre, 2010).

0.6.4 Approche statistique

Cette thèse combine des analyses effectuées sur des données de composition, ainsi que de diversité alpha et bêta, sous des dimensions taxonomiques et fonctionnelles. Pour évaluer l'effet des divisions régionales ou de l'impact humain sur la composition taxonomique et fonctionnelle des communautés, une approche par analyse canonique de coordonnées principales a été utilisée (CAP; chapitres I et III). Pour relier ces mêmes compositions aux variables environnementales, nous avons utilisé l'analyse canonique de redondance (RDA) et le partitionnement de la variance (chapitre II). Pour visualiser les indices de diversité en fonction de l'espace (chapitre I), de l'environnement (chapitre II) et de l'utilisation du sol (chapitre III), des analyses en composantes principales (ACP) ont été effectuées. Pour analyser les réponses de la diversité taxonomique et fonctionnelle des communautés de zooplancton aux variables environnementales (chapitre II), deux approches complémentaires ont été utilisées. D'abord, les seuils environnementaux ont été établis avec des arbres de régression univariés, puis les variations de diversité ont été modélisées par une combinaison de Random Forest et de modèles additifs généralisés mixtes. Pour évaluer l'homogénéisation spatiale (chapitres I et III) et temporelle (chapitre III) des communautés, nous avons estimé la diversité bêta taxonomique et fonctionnelle, ainsi que la contribution des espèces ou des sites à cette diversité. Finalement, la diversité bêta temporelle taxonomique et fonctionnelle a été liée aux différents types d'utilisation du sol avec des arbres de régression univariés (chapitre III).

CHAPITRE 1

MULTI-SCALE BIODIVERSITY ANALYSES IDENTIFY THE IMPORTANCE OF CONTINENTAL WATERSHEDS IN SHAPING LAKE ZOOPLANKTON BIOGEOGRAPHY

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Cindy Paquette[1,2,3], Irene Gregory-Eaves[2,3] and Beatrix E. Beisner[1,2]

Corresponding author: paquette.cindy@courrier.uqam.ca

[1]Department of Biological Sciences, University of Quebec at Montreal, Montreal, Quebec, Canada;
[2]Interuniversity Research Group in Limnology (Groupe de recherche interuniversitaire en limnologie; GRIL);
[3]Department of Biology, McGill University, Montreal, Quebec, Canada

1.1 Abstract

Aim: We examined variation in crustacean zooplankton composition and diversity across Canada, the most-lake rich country in the world. In addition to α-diversity patterns, we explore mechanisms behind β-diversity spatial variation, using taxonomic and functional metrics. Our goal was to explore geographical gradients and related mechanisms shaping zooplankton distribution across different spatial scales.

Location: Canada.

Taxon: Crustacean zooplankton.

Methods: Pelagic zooplankton was sampled in and characterized for 624 lakes across Canada, spanning 12 ecozones (defined by climatic, vegetation and geological differences) or 6 continental drainage basins as part of the NSERC Canadian Lake Pulse Network project. We compared taxon and trait distributions, as well as spatial (longitudinal and latitudinal) patterns of community composition and diversity. We computed taxonomic and functional spatial β-diversity indices, decomposing these into taxon replacement and richness differences. Finally, species (or traits) and lake uniqueness (contributions) to β-diversity (SCBD and LCBD) were estimated by ecozone and continental basin.

Results: 90 crustacean zooplankton species were identified across the country. Differences in zooplankton taxonomic and functional composition were more distinct when considered by continental basin than by ecozone. α-diversity varied greatly across space, with greatest diversity in eastern Canada. β-diversity was greatest when based on taxonomy and was driven by richness differences across all spatial and biodiversity dimensions.

Main conclusions: Structuring factors influencing zooplankton taxon and trait assemblages vary across spatial scales, being more important at the broadest scale considering continental hydrodynamics. Our results point to the combined effects of physical barriers to longitudinal dispersal and climate change in shaping zooplankton taxonomic and functional biogeography across Canadian lakes.

1.2 Introduction

Determining species distributions across regions and the factors affecting these are major questions in ecology and biogeography (Lomolino *et al.,* 2010; Smith *et al*., 2020). Indeed, species distribution is not random and each species has a different ecological niche depending on their specific tolerance or sensitivity to a variety of aquatic environments (Korhola et Rautio, 2001). Which taxa or functional traits are found in a location depends on three core community ecology factors: dispersal, abiotic conditions and biotic conditions (Thompson *et al.*, 2020). While abiotic and biotic conditions related to the local environment will influence species survival in place, stochastic dispersal connects metacommunities via immigration and emigration (Leibold *et al.*, 2004). However, previous studies have shown that the importance of abiotic and biotic environmental variables relative to spatial dispersal decreases with increasing spatial extent (Meynard *et al.,* 2013; Gonçalves-Souza *et al.*, 2014; Lansac-Tôha *et al.*, 2020). Given the large spatial scale of our study, covering lakes across one of the largest countries in the world and multiple ecozones, dispersal-related processes will be the focus of the biogeographical patterns explored. Much work in large-scale biogeographical research has been conducted on macroscopic plants and animals (e.g., Olden et al., 2010; Swenson *et al*., 2011), while lower trophic groups in aquatic ecosystems are generally underrepresented, and efforts are still needed to fill this gap (Heino, 2011; Pinel-Alloul *et al*., 2021). Our goal was thus to identify biodiverse regions and to quantify the relative importance of different spatial scales of organization for zooplankton lake communities across Canada, one of the largest but also most lake-rich countries globally.

Lake zooplankton communities provide an ideal system for the study of dispersal limitation as they provide a simple model of passive animal dispersal. Moreover, changes in zooplankton communities can be interpreted as a warning sign of perturbation and can be critical to whole lake ecosystem functioning given their central food web position (Xiong *et al.*, 2020). The distribution of crustacean zooplankton in lakes is shaped by both local environmental drivers and spatial factors limiting their dispersal capacity (Beisner *et al.*, 2006; De Bie *et al*., 2012; Padial *et al.*, 2014). Zooplankton in southern Canada appear to disperse equally well by watercourses as they do overland (e.g., wind or animal vectors), likely primarily via dormant stages (Beisner *et al.*, 2006). Across North American lakes, plankton have also shown important responses to large-scale environmental gradients (Stomp *et al.,* 2011; Vyverman *et al.*, 2007; Sodré *et al.,* 2020). Distributions and structural considerations of crustacean zooplankton taxa and functional traits can provide information about changes occurring within individual lakes, but are also ideal for assessing ecological shifts at large spatial scales more generally in aquatic communities (Pinel-Alloul et al., 2013; Griffiths et al., 2019). In the context of increasing anthropogenic pressure, baseline data enabling the detection of changes in lakes over time as early-warning signals are needed.

In addition to composition, diversity indicators such as α- and β-diversity are informative for the study of biogeographical gradients (Whittaker, 1972; Norris, 2000; Mittelbach *et al*., 2007; Kraft *et al*., 2011). Previous work on zooplankton demonstrated that at the continental scale, solar radiation was among the most important predictors of taxonomic richness across Canadian lakes, a trend associated with the richness-energy hypothesis (Pinel-Alloul *et al*., 2013). β-diversity has been increasingly useful as a conservation and biodiversity management tool as it can identify key taxa (via species contribution to β-diversity; SCBD) or sites (local contribution to β-diversity; LCBD) that substantially enrich regional diversity (Legendre et De Cáceres, 2013). Because taxon compositional shifts are more common with anthropogenic change than are losses per se (Vellend *et al*., 2013; Dornelas *et al*., 2014), β-diversity can reveal biodiversity shifts that remain undetected with α-diversity (Winegardner *et al*., 2017). Furthermore, β-diversity can be decomposed into differences in composition (species substitution, turnover) and richness gradients (gain or loss of individuals, species nestedness) (Legendre, 2014). Finally, earlier work has shown that functional β-diversity can be more strongly related to ecosystem functioning and ecological niches than are more traditional diversity indices (Jones *et al*., 2019; García-Girón *et al.*, 2020;). We thus used a multi-metric approach to develop the most sensitive indicators of variation in zooplankton assemblages across critical spatial ecological units.

A large national sampling effort of > 600 lakes spanning many biogeoclimatic zones via the NSERC Canadian Lake Pulse Network provided a unique opportunity to advance knowledge on crustacean zooplankton biogeography by considering a suite of diversity and compositional metrics. Home to the largest quantity and surface area of lakes in the world (Messager *et al*., 2016), Canada is ideal to assess large scale distribution patterns owning to its important heterogeneity in terms of landforms, soils, water features, vegetation, climate and human activities. Previously, biogeographical studies in North American or European lakes have focused on spatial patterns in zooplankton species composition (e.g., Patalas *et al.* 1994; Pinel-Alloul *et al*., 2013; Marrone *et al*., 2017; Stoch *et al*., 2019; Dexter *et al*., 2020), but such a conventional approach does not consider functional redundancy among taxa (but see Sodré *et al.*, 2020). Additionally, at the largest spatial extents, corresponding to ecozones or continental basins, it remains an open question whether taxonomic and functional zooplankton distribution and diversity variation in α- or β-diversity respond similarly.

Our study examined zooplankton taxonomic and functional composition distribution patterns; the first pan-Canadian analysis of zooplankton functional trait variation. We examined three main hypotheses (Table 1.1). We hypothesized that (a) the larger scale continental basins would structure zooplankton communities more than would the smaller scale ecozone classifications. Continental basins represent large-scale hydrodynamics and should drive more aquatic zooplankton dispersal across lakes than an ecozone classification that characterizes mainly environmental gradients such as vegetation, geological and climate typologies. Second, we tested the richness-energy hypothesis and expected (b) that lakes in southern regions would harbour greater taxonomic α-diversities (Pinel-Alloul *et al.*, 2013). However, we expected that functional diversity should remain more constant than taxonomic diversity across regions, because of species redundancy in functional traits (Barnett *et al.*, 2007). Finally, we evaluated the degree of spatial heterogeneity (β-diversity) and tested whether taxonomic or functional approaches better explained spatial variation, region uniqueness and individual species or traits influences on β-diversity. Our last hypothesis (c) was that taxonomic β-diversity should demonstrate greater variation than functional trait β-diversity because of more limited species dispersal at this large spatial scale.

Table 1.1 Overview of the hypotheses, associated analyses and main results of the study of the biogeography of zooplankton in Canadian lakes. See the main text for details.

Hypothesis	Analysis	Main result
(a) Continental basin is stronger factor structuring zooplankton than ecozones	• CAP analysis	• Continental divides explain more variation in taxonomic and functional composition
(b) Greater α-diversity in southern Canada	• Map with PCA scores • PCA with α-diversity metrics and lake coordinates • ANOVA on α-diversity by ecozone and continental basins	• Greater α-diversity in eastern Canada • Longitudinal rather than latitudinal trend in α-diversity
(c) Taxonomic β-diversity varies more than functional β-diversity	• Total β-diversity by ecozone and basin • ANOVA on LCBD with ecozone and continental basins • Taxonomic and functional SCBD	• Greater taxonomic than functional β-diversity • Dominated by richness difference component • Functional SCBD more useful for conservation

1.3 Material and Methods

1.3.1 Data set

Over three summers (2017-2019), 664 lakes were sampled across 12 different ecozones and 6 continental basins across Canada following a standardized protocol developed by the NSERC Canadian Lake Pulse Network (see Huot *et al.*, 2019). All lakes within 1 km of roads were selected randomly with a factorial design according to lake size (three size classes: 0.1-1km^2, 1-10km^2, 10-100km^2) and human impact (three classes of land-use in the watershed: low, medium, high; defined in Annexe A). “Core” ecozones experienced the most extensive sampling (Pacific Maritime, Montane Cordillera, Semi-Arid Plateaux, Boreal Plains, Prairies, Boreal Shield, Mixedwood Plains, Atlantic Highlands and Atlantic Maritime). In the remaining ecozones (Boreal Cordillera, Taiga Cordillera, Taiga Plains), fewer lakes were sampled due to limited road access. The six continental drainage basins represented in our dataset were Pacific Ocean, Arctic Ocean, Hudson Bay, Gulf of Mexico, Great Lakes-St. Lawrence and Atlantic Ocean. These continental watersheds were delimited by the National Hydrographic Network watershed data and represent landscape surfaces where precipitation and river systems drain to distinct gulfs, seas or oceans.

1.3.2 Zooplankton sampling and identification

At the deepest point in each lake, we collected integrated water column zooplankton samples using a 100µm mesh Wisconsin net. Samples were treated on site with an initial CO_2 narcotization, and then preserved in 70% ethanol. Samples were stored at room temperature and identified to species by BSA Environmental Services (Ohio, U.S.A.). BSA also estimated biomasses using the average length of up to 10 measured individuals per taxon per lake and pre-established size/weight relationships for each species (Dumont *et al*., 1975; McCauley, 1984; Lawrence *et al*., 1987) (see Annexe B for details). Our final dataset consisted of 624 lakes across 12 ecozones and 6 continental basins (Figure 1.1), spanning a large range of lake size, depth and human impact (Annexe S3). Analysis of Variance (ANOVA) was used to determine the effects of ecozones and continental basins on mean total lake biomasses.

Taxa were classified functionally using species-specific traits from the literature (Demott et Kerfoot, 1982; Barnett *et al.*, 2007; Griffiths *et al.*, 2019). The traits used were: resource acquisition (B(*Bosmina*)-filtration, C(*Chydorus*)-filtration, D(*Daphia*)-filtration, S(*Sidae*)-filtration, stationary suspension or raptorial), habitat (littoral, pelagic or intermediate) and trophic group (carnivore, herbivore, omnivore, or a combination of these). Species mean size represents an integrative trait related to predation, resource acquisition, productivity and competitive strength (Brooks et Dodson, 1965; Barnett *et al.*, 2007; Litchman *et al*., 2013; Hébert *et al*., 2017). Size was used as a continuous trait in all diversity analyses. However, to estimate size-based distributions, a cutoff of 0.5 mm was used to create two size classes (small and large) to roughly balance the number of species per size class.

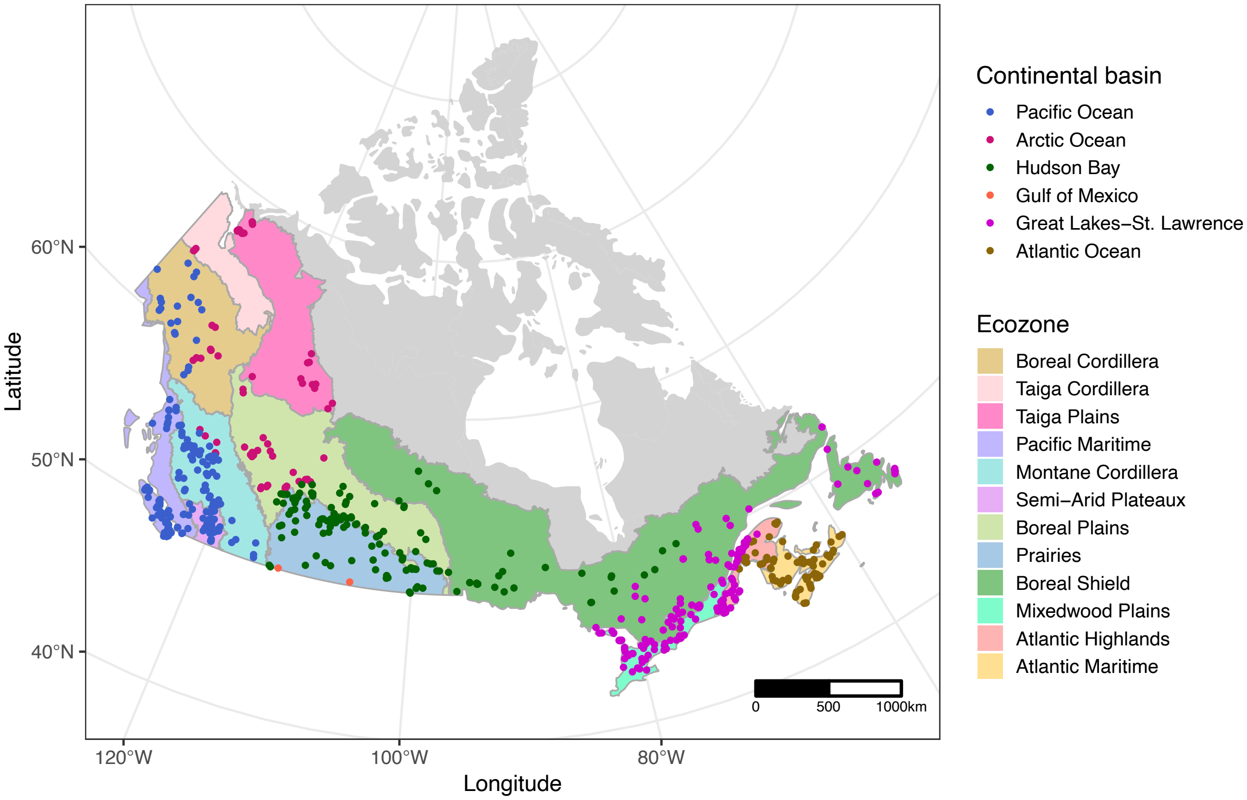

Figure 1.1 Map of lakes sampled as part of the NSERC Canadian Lake Pulse Network for pelagic zooplankton (n=624). Lakes are contoured by ecozone and colored by continental basin. Regions are listed from west to east. The map was created using Canada Atlas Lambert (NAD83 CSRS).

1.3.3 Estimating distribution patterns and spatial distinctness

Maps for each taxon were produced to visualise distribution patterns (Annexe D). Species occurrences by lake were represented in a rank-frequency diagram. Relative biomass composition by genus and by categorical trait were examined by ecozone and continental basin, where rare genera (< 2% relative biomass in all lakes) were grouped in category “other”. Based on similarity observed via the relative biomass composition by taxa and traits, the Taiga Cordillera (n=3) and Taiga Plains (n=22) were combined, as were the continental basins Gulf of Mexico (n=2) and Hudson Bay (n=145); roughly balancing the number of lakes across groups (Annexe C).

Multivariate analyses were used to reveal patterns in the compositional datasets. We used canonical analysis of principal coordinates (CAP) to assess the distinctness of zooplankton species or categorical functional traits across regions. Hellinger-transformed total biomasses of common taxa (defined as those with >2% relative biomass in at least one lake) were used with the *CAPdiscrim()* function of the BiodiversityR package (Kindt, 2020). The *CAPdiscrim()* function returns the percentage of correct predictions of the full model (i.e. percentage of lakes that were classified in the correct region based on taxon or trait composition), as well as by ecozone or continental basin. A multivariate analysis of variance (MANOVA) within this function then assessed regional classification significance. To enable comparison of CAP classifications at different regional scale groupings (differing in both the number and sizes of groups by ecozone or continental basin), the adjusted % predicted was estimated as the percentage of correct allocations minus the percentage of correct allocations that could be attributed to a randomly correct prediction (adjusted % predicted = % correct allocations - (100/N); where N is the number of groups).

1.3.4 Estimating spatial patterns in α- diversity

Using biomass and taxonomic composition data, we estimated the most common diversity indices (Hill, 1973): species richness, Shannon entropy, Simpson diversity and Pielou's evenness (using *diversity()* in vegan package; Oksanen *et al.*, 2019). Rarefied species richness was calculated using *rarefy()*, rounded to 109 individuals (lowest count size). For functional diversity, we estimated functional evenness (*FEve*; Villéger *et al*., 2008), functional dispersion (FDis; Laliberté et Legendre, 2010) and functional richness (FRic; Villéger *et al.*, 2008). These were computed using the *dbFD()* function with Gower distances in the FD package (Laliberté *et al.*, 2014).

To visualise spatial patterns in species composition and categorical functional traits across Canada, the lake scores from the first axis of principal component analyses (PCA) were used to produce heat-maps. To illustrate spatial patterns in α-diversity metrics, a PCA with lake longitude and latitude values was computed. The taxonomic and functional diversity metrics were then added passively to the plot to visualise correlations with the lake coordinates scores.

1.3.5 Estimating β-diversity

β-diversity was used to compare species composition and functional traits by site across the country, within ecozones and continental basins. We differentiated the country-wide, within ecozones or continental basins total β-diversity into either the taxon replacement component (turnover; i.e. sites are most different in terms of species composition) or the richness difference component (nestedness; i.e. main differences between sites results from the number of species present) (Baselga, 2012; Villéger *et al.*, 2013).

We estimated taxonomic total β-diversity, turnover, nestedness, local contribution to β-diversity (LCBD) and species contribution to β-diversity (SCBD) using species data with the functions *beta.div()* and *beta.div.comp()* in the adespatial package (Legendre et De Cáceres, 2013; Legendre, 2014). Taxonomic β-diversity and LCBD were computed with the percentage-difference Podani index, while SCBD was computed on the Hellinger-transformed biomass species data (as described by Legendre et De Cáceres, 2013). Significance of LCBD values was assessed using site shuffle null models, part of the *beta.div()* function, indicating which communities differed from those expected by chance at $\alpha \leq 0.05$ (Legendre et De Cáceres, 2013). The significance of LCBD values for each lake was assessed using the permutational *p*-value (permutations = 9,999). To test for significant LCBD sites after correcting for multiple-testing, we used Holm's procedure (see Borcard *et al*., 2018; p. 308). Critical species were identified as those having values larger than across-site mean SCBD values (as in Borcard *et al*., 2018; p. 386).

Total functional β-diversity and its decomposition into turnover and nestedness was estimated using *multidimFbetaD()* function (Villéger *et al*., 2008, 2013) with species presence-absence data from 613 lakes (nine lakes with only one species had to be removed from the analysis) and species coordinates along the two first axes of the functional space. Functional LCBD values were obtained using *LCBD.comp()* from adespatial package (Legendre et De Cáceres, 2013; Legendre, 2014) and the total β-diversity dissimilarity matrix computed previously using *multidimFbetaD().* Species contribution for functional β-diversity (functional equivalent of SCBD) was computed with *beta.div()* on Chord-transformed trait-weighted species composition according to the method developed by Nakamura *et al.* (2020).

Mean values of α-diversity and LCBD across lakes were compared by ecozone and continental basin using ANOVA. Significant mean pair-wise differences among ecozones and among continental basins were identified using a *TukeyHSD()* post-hoc test. Relative mean values of total biomass, taxonomic and functional α-diversity, as well as taxonomic and functional β-diversity were represented in radar charts by ecozone and continental basin. All statistical analyses were performed in R v. 3.6.3 (R Core Team, 2020).

1.4 Results

1.4.1 Distribution patterns and spatial distinctness of taxonomic and functional composition

Crustacean zooplankton biomass and composition varied substantially across Canada. Zooplankton biomass was significantly different among ecozones and continental basins ($p<2e\text{-}16$, Figure 1.2a, Annexe E), with the largest values observed in central Canada, in the Prairies ecozone (mean biomass per lake = 1738.1 ± 341.89 µg d.w./L) and the Hudson Bay continental basin (mean biomass per lake = 1091.0 ± 185. µg d.w./L). Across all lakes, 90 crustacean zooplankton species were identified (distribution maps in Annexe D). *Bosmina longirostris* was the most frequently found crustacean zooplankton (55% of the lakes, Annexe F). The invasive cladoceran *Eubosmina coregoni* occurred in 3% of lakes and only in eastern Canada.

Daphnia was the dominant genus in 8 of the 12 ecozones, with a relative contribution to total biomass generally decreasing from west to east, and lower abundances in northwestern regions (Taiga and Boreal Cordillera, and the Taiga Plains; Figure 1.3a,b). In these northern ecozones, *Leptodiatomus* contributed most to total biomass. The Atlantic Highlands ecozone was unique in Canada with *Eubosmina* dominating, although this pattern likely resulted from extreme biomass values (87% of biomass) of *Eubosmina coregoni* in one hypereutrophic lake. The relative biomass of functional trait groupings (Figure 1.3c,d) was more similar across the landscape than for genera. The most common feeding types were stationary suspension, D-filtration and raptorial. Pelagic zooplankton were uniformly dominant, as would be expected from the sampling methodology. Herbivores were the most dominant trophic type across ecozones as were small zooplankton (<0.5 mm). Similar results were reflected among continental basins (Figure 1.3d).

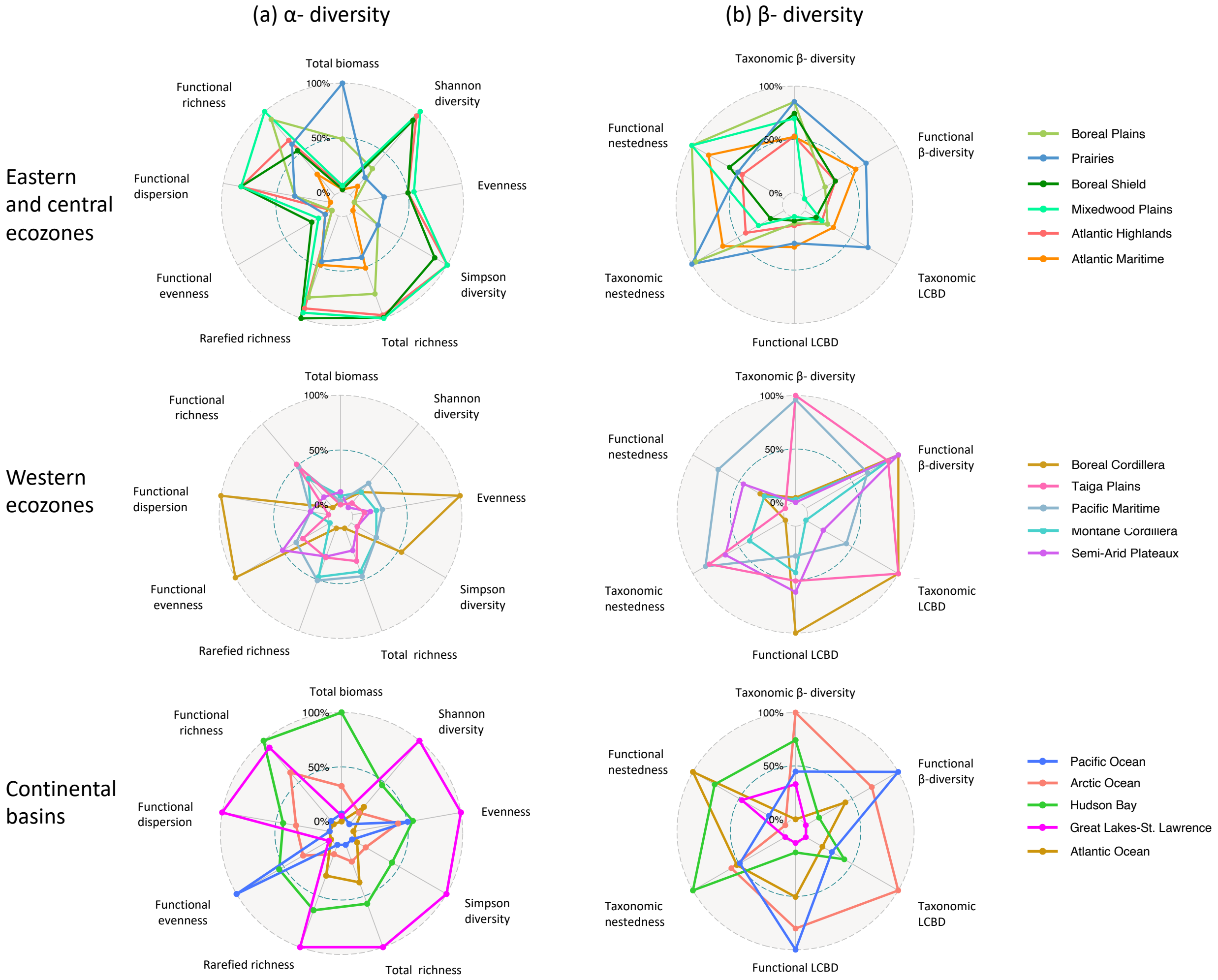

Figure 1.2 Radar charts showing relative values (rescaled from 0 to 100%) of total biomass and mean values of α- (a) and β- (b) diversity by ecozone of crustacean zooplankton from 624 Canadian lakes (western and central/eastern ecozones illustrated separately; although the rescaling was done on the full ecozone dataset) and continental basin. LCBD refers to local contributions to β-diversity. Nestedness (richness difference) values are relativized to total β-diversity (nestedness + replacement components).

Canonical analyses of principal components (CAP) were used to reveal spatial patterns in zooplankton taxa or functional traits and ecozones or continental basins (Figure 1.4). All four MANOVA models tested were significant (Table 1.2), indicating significant differences of species and trait composition among regions. For both taxonomic and functional analyses, the percentage of lakes correctly attributed to the appropriate region according to their species or trait composition (% correct attribution) was greater using continental basins (61.1% and 42.0%

respectively) than ecozones (46.3% and 29.0% respectively), even after correcting for the number of groups (Adjusted % predicted, Table 1.2).

1.4.2 Spatial patterns in total biomass and α-diversity

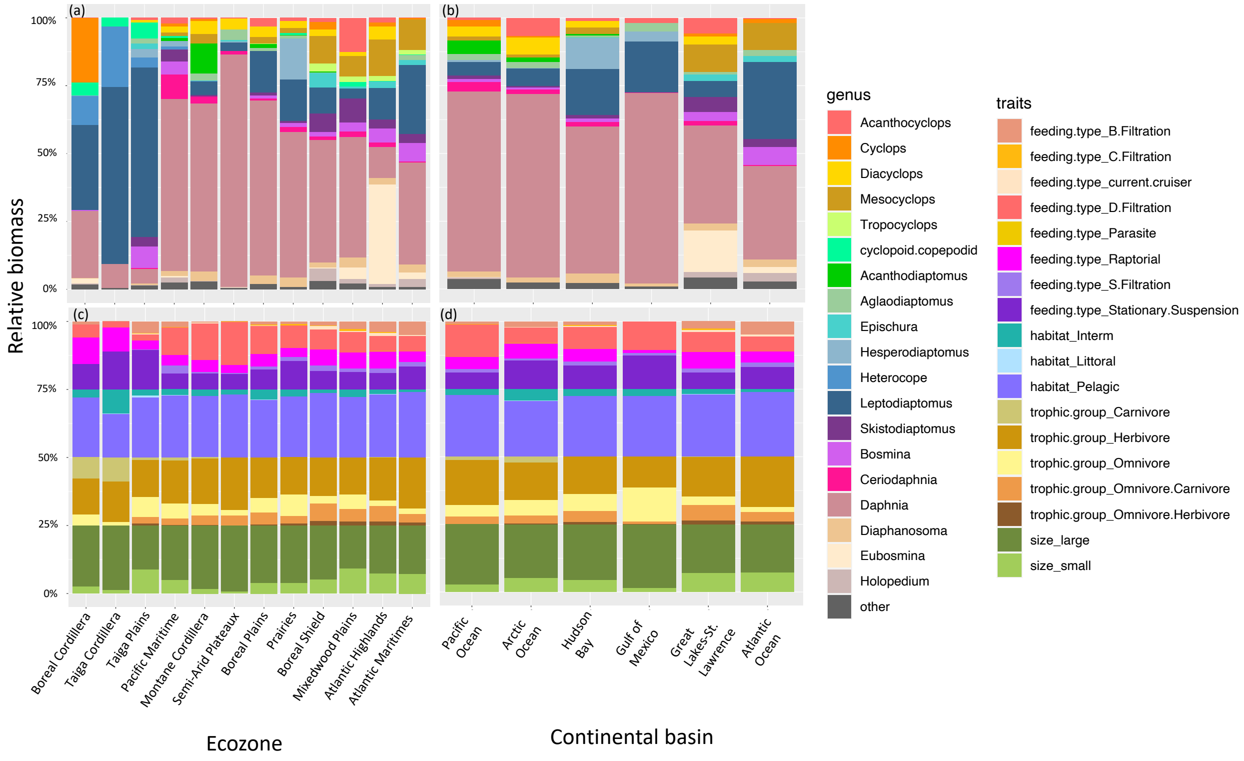

Figure 1.3 Relative biomass of zooplankton genera (a,b) and functional traits (c,d) relative biomass by ecozone and continental basin across Canada. Rare genera (relative biomass <2% in at least one ecozone or continental basin) are grouped in "other".

Taxonomic and functional α-diversity also varied considerably across space (Figure 1.2a, Annexe E), with overall greater diversity in eastern Canada. All taxonomic diversity indices varied significantly across ecozones ($p<0.05$), and all but evenness varied across continental basins ($p<0.001$). Overall, total and rarefied species richness varied the most among ecozones ($p < 2e\text{-}16$). Mean richness across all lakes was 7 taxa (varying from 2 to 16 species) and 6 functional traits (varying from 1 to 12 unique trait combinations; excluding species size, data not shown). Taxonomic richness, Simpson, and Shannon indices were all significantly greater in the Boreal Shield, Mixedwood Plains and Atlantic Highlands ecozones and in the Great lakes-St. Lawrence basin. The PCA ordination with lake coordinates revealed strong associations between most of the α-diversity (Shannon and Simpson diversity, richness, rarefied richness and *FDis*) indices and longitude (Figure E.6 in Annexe E).

A clear longitudinal pattern was observed in lake PCA data based on the first axis scores derived from the species biomass matrix (Figure 1.5a). Lakes with negative scores were typically found in the western and central Canada, while positive scores were concentrated in eastern Canada. A longitudinally distinct pattern was weaker for functional trait biomass PCA scores (Figure 1.5b).

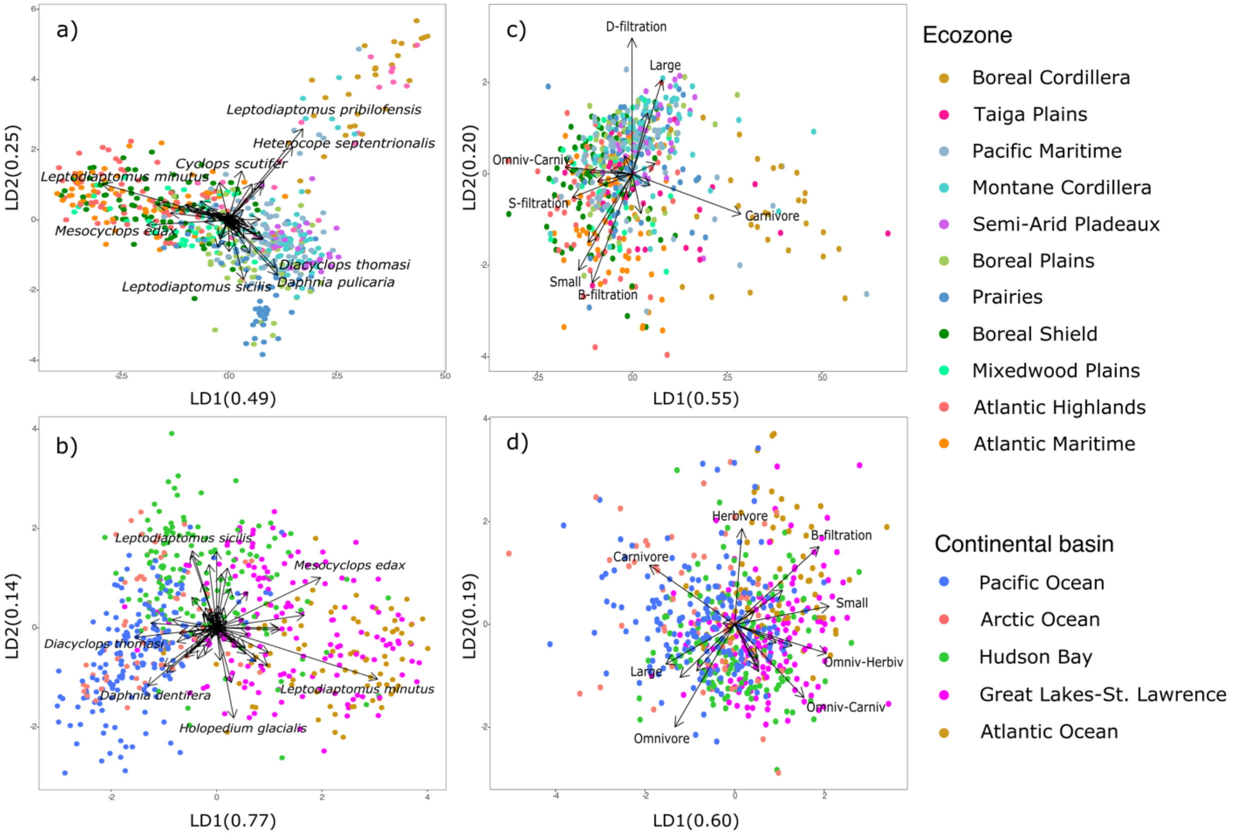

Figure 1.4 Canonical Analysis of Principal Coordinates based on Discriminant Analysis (CAP, Scaling = 1) assessing the distinctness of Canadian zooplankton composition (a,c) and functional traits (b,d) in the different ecozones and continental basins. The proportion of the among-group variance explained is displayed by each of the linear discriminant axes.

Table 1.2 Percentages of correct allocation, p-values and random-corrected percentages from the species and trait Canonical Analysis of Principal Coordinates (CAP) analyses by ecozone (a) and continental basin (b) of crustacean zooplankton in 624 Canadian lakes.

(A) cap by ecozone	**Taxonomic % correct attribution**	**Functional % correct attribution**
All	46.3	29.0
Boreal Cordillera	**83.3**	**76.7**
Taiga Plains	20.0	8.0
Pacific Maritime	52.2	33.3
Montane Cordillera	62.7	50.8
Semi-Arid Plateaux	36.4	0.00
Boreal Plains	43.5	11.6
Prairies	49.3	25.4
Boreal Shield	25.9	40.0
Mixedwood Plains	54.7	22.6
Atlantic Highlands	23.8	7.9
Atlantic Maritime	63.5	38.1
p-value	<2.2e-16	<2.2e-16
Adjusted % predicted	36.9	19.9

(b) CAP by continental basin	**Taxonomic % correct attribution**	**Functional % correct attribution**
All	61.1	42.0
Pacific Ocean	77.1	59.6
Arctic Ocean	37.9	22.7
Hudson Bay	60.6	23.2
Great Lakes-St. Lawrence	56.6	52.0
Atlantic Ocean	53.1	32.1
p-value	<2.2e-16	<2.2e-16
Adjusted %	41.1	22.0

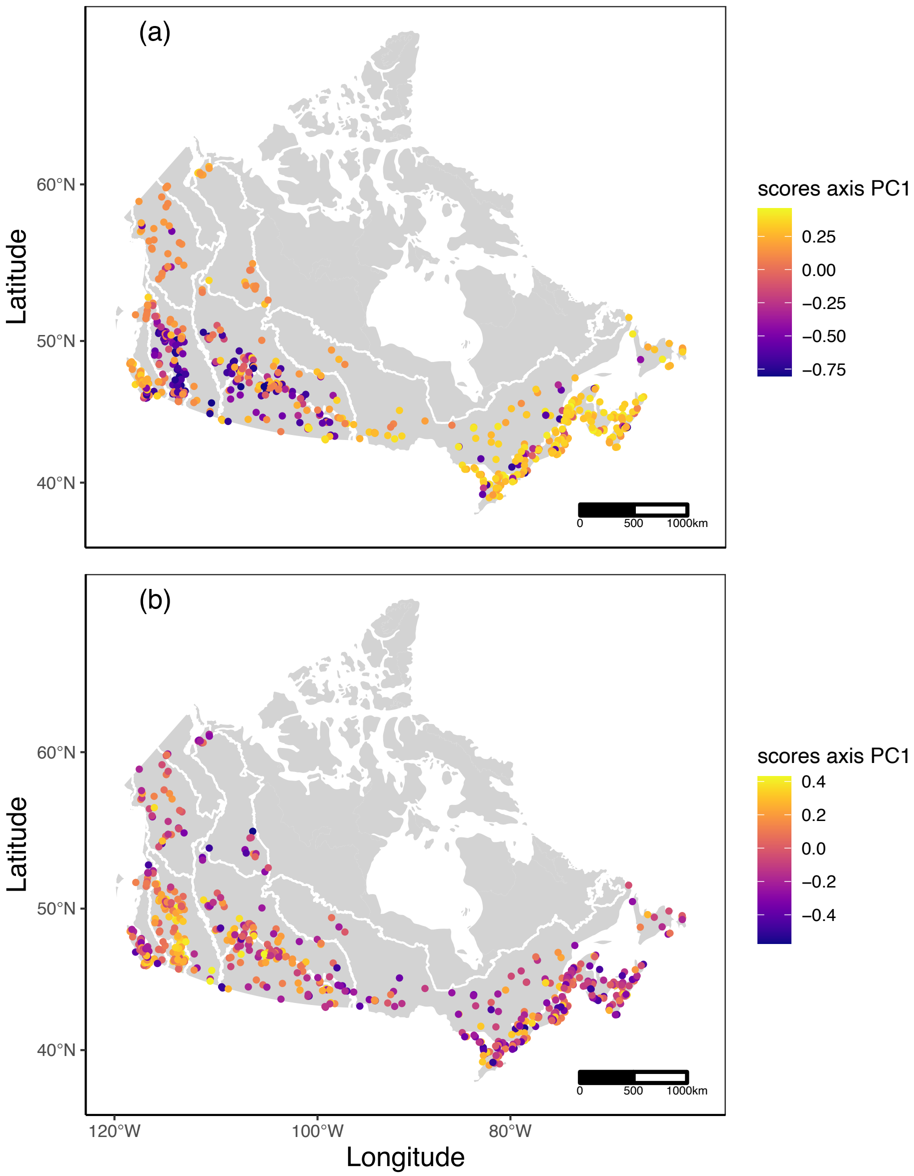

Figure 1.5 Axis 1 scores of Principal Component Analysis (PCA) applied on Hellinger-transformed biomass data of species (a) or functional traits (b) of crustacean zooplankton in Canadian lakes. The maps were created using Canada Atlas Lambert projection (NAD83 CSRS).

1.4.3 Spatial β-diversity

Comparing across all sites, taxonomic and functional β-diversity were 0.47 and 0.32, respectively (Annexe G). Richness difference (nestedness) was the dominant mechanism of compositional change among all lakes. The relative contribution of richness differences to among-lake β-diversity was 0.63 for taxonomic and 0.52 for functional trait estimates (Annexe G).

Taxonomic and functional and LCBD values varied significantly among ecozones (*p* <2e-16) and continental basins (*p*<0.001). The northern-most ecozones (Boreal Cordillera and Taiga Plains) had the largest taxonomic LCBD values; for continental basins it was the Arctic Ocean (Figure 1.2b and Figure G.1 in Annexe G). At an individual site level, 62 lakes were identified as having significant LCBD (without correction for multiple comparison, Figure 1.6). There was a clear pattern of more sites in western and northern Canada with significant LCBD. After correcting for multiple testing, no site had a significant value. For functional LCBD, the Taiga Plains ecozone, as well as the Pacific Ocean basin contained lakes with the greatest contribution to local diversity on average (Figure 1.2b, Figure G.1).

In all, twenty-seven key species were identified, with SCBD values larger than the national taxonomic SCBD mean (Table G.3 in Annexe G). *Daphnia pulicaria* contributed the most of any species to β-diversity. Functional traits were also used to estimate species contributing the most to functional β-diversity. Fifty species contributed more to functional SCBD the national mean, with *Bosmina longirostris* contributing the most.

1.5 Discussion

Our study provides one of the most intensive and extensive analyses of biogeographical patterns of crustacean zooplankton by considering both taxonomic and functional biodiversity dimensions across lakes covering the east-west axis of the second largest country in the world. This approach clearly identified trends in zooplankton composition among continental basins and ecozones, as well as differences across a suite of diversity metrics. Overall, we found support for most of our hypotheses, and were able to build upon previous studies of zooplankton biogeography, bringing novel insights into the role of large-scale patterns and drivers (Table 1.1).

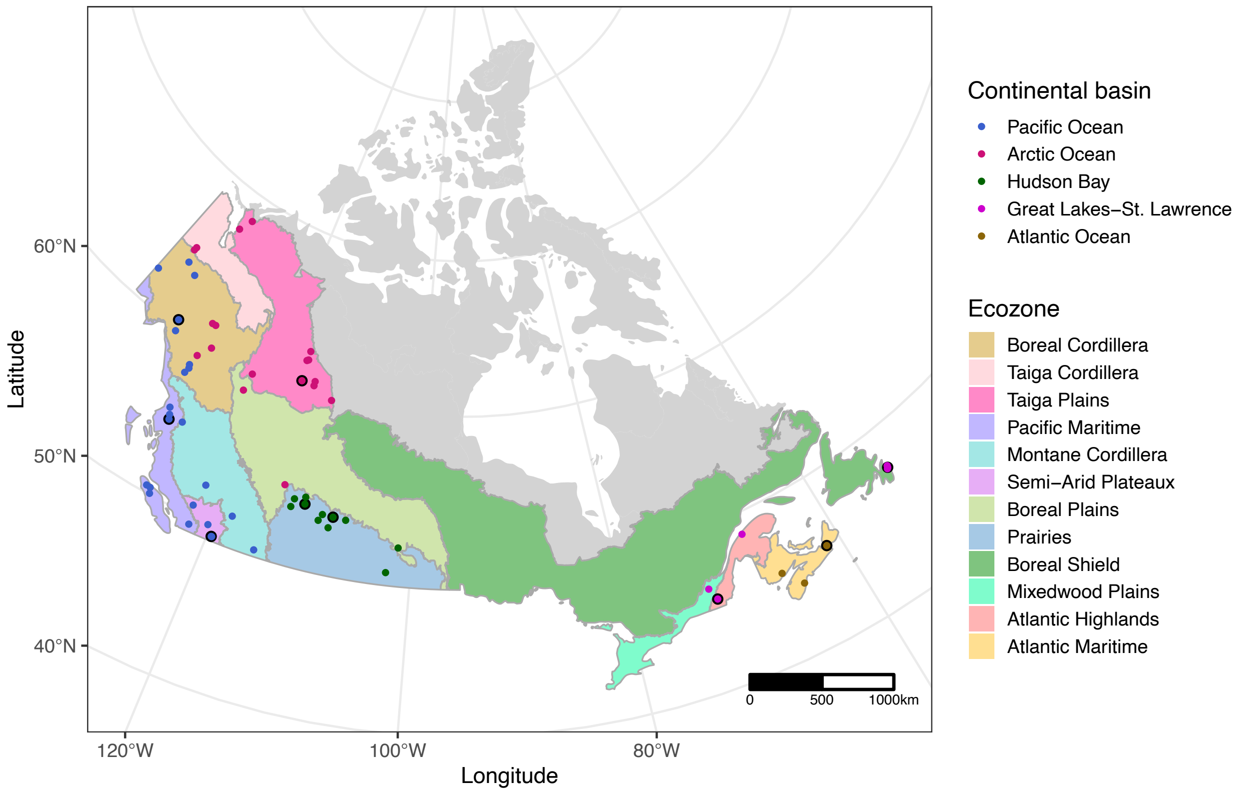

Figure 1.6 Map of Canadian lakes with significant local contributions to β-diversity (LCBD) values (n=62) for crustacean zooplankton. Sites are contoured by ecozone and colored by continental basin. After correcting for multiple comparisons, no sites remained significant at *p*<0.05; although the 9 sites circled in black were borderline significant (*p*=0.06). The map was created using Canada Atlas Lambert projection (NAD83 CSRS).

1.5.1 The role of spatial extent

Our first major goal was to identify at which scale, the regional ecozone level or larger scale continental basin, would zooplankton community composition and functional traits be most differentiated. Both taxonomic composition and functional trait regional distinctness (CAP analyses) were ~15% stronger for continental basins than for ecozones, in agreement with our original hypothesis. Based on watercourse distributions and hydrological flows, we had hypothesized that the continental basin framework would be a stronger structuring determinant than ecozones (Table 1.1). Our results also concord with previous work demonstrating that factors influencing zooplankton community structure vary across spatial scales, and that at the broadest scale, continental hydrodynamics become increasingly important for zooplankton biomass or diversity, while habitat variables are relatively stronger at smaller scales (Mackas *et al*., 1985; Borcard *et al*., 2004; Declerck *et al.*, 2011; Anas *et al*., 2017). Similarly, Bennett *et al.* (2010) and Vilmi *et al*. (2017) reported that lake diatom patterns were mainly driven by space rather than environmental factors at the larger scales. Most previous studies were conducted at smaller spatial scales than ours, and thus the distinctness detected among ecozones and continental basins herein extend these findings to continental scales. Functional trait allocation at both spatial scales was weaker than that based on taxonomy; this pattern is likely driven by the redundancy of functional traits at this large spatial extent.

1.5.2 Latitudinal and longitudinal patterns

The most evident pattern in diversity and composition that we observed in the country-wide data was a longitudinal one, with more diverse, but less unique zooplankton communities across eastern Canada. Indeed, all taxonomic α-diversity indices were greater in the eastern regions: Boreal Shield, Mixedwood Plains and in the Atlantic Highlands ecozones, as well as in the Great Lakes-St. Lawrence continental basin. Significant local contributions to β-diversity (LCBD) sites were also relatively scarce in eastern Canada, indicating that while being more species-rich, the communities are relatively homogeneous.

There are several potential mechanisms to support the apparent longitudinal trend. One main mechanism invokes the relative lack of physical barriers to dispersal in eastern Canada compared to the more mountainous west. Important physical or environmental barriers could limit species dispersal such that some central and eastern species might not be able to reach or survive in northern and western lakes. For example, the Rocky Mountains likely isolate lakes from the Pacific Ocean divide, and colder temperatures in the north might not provide a suitable habitat for southern species. Zooplankton dispersal limitation by mountain chain barriers was similarly suggested to influence copepod diversity in the Western Palearctic (Marrone *et al.*, 2017). Moreover, the prevailing westerlies (winds moving air from west to east) in Canada could lead to this pattern, with lakes in the eastern part of the country being exposed to greater potential immigration of freshwater zooplankton. This hypothesized mechanism is further supported by the canonical analysis of principal coordinates (CAP) results, indicating that lakes from the Pacific Ocean divide and from the Boreal Cordillera ecozone have very distinct species and traits, while eastern regions are less distinctly defined (Table 1.2). A distinct longitudinal pattern was also observed across lake PCA scores based on species biomass data (weaker for functional trait biomass), where eastern Canadian lakes were very distinct from western ones (Figure 1.5). Interestingly, these geographic results cannot be explained by lake morphometric differences whereby deeper lakes can host more vertical habitat niches (Jeppesen *et al.*, 2000; Barnett et Beisner, 2007; Longhi et Beisner, 2010). Deep lakes are found both in western and eastern Canada.

We noted a trend toward greater, but not significant, mean taxonomic and trait (*FRic*) richness in the Mixedwood Plains, Canada's southernmost ecozone, partially supporting our second hypothesis (Table 1.1). This hypothesis was informed by earlier analyses of zooplankton in 1665 Canadian lakes, where Pinel-Alloul *et al.* (2013) attributed greater taxonomic richness in southern regions to the richness-energy hypothesis (Brown, 1981; Wright, 1983) that stipulates co-existing species richness is driven by available energy (e.g., solar radiation). However, Pinel-Alloul *et al.* (2013) did not include diversity indicators weighted by abundance, biomass or based on functional traits. Furthermore, their sampling was done over three decades, which in itself could introduce artefacts such as varying responses to acidification or climate change. Determining whether the non-significant trends we observed are a consequence of the richness-energy relationship, or an indirect effect of higher productivity and greater nutrient loading in highly populated regions of the Mixedwood Plains (Gibbs *et al*., 2009; Chambers *et al*., 2012) would necessitate further investigation into local habitat factors. Moreover, the association between α-diversity indices and lake coordinates visualized with a PCA ordination (Figure E.6 in Annexe E) revealed strong congruence between numerous α-diversity indices and longitude rather than latitude, implying that an energetic explanation is unlikely of primary significance. On the other hand, functional diversity indices were not as strongly related to longitude, and they varied less spatially compared to taxonomic indices (Figure 1.3 and 1.5). Overall, the spatial patterns observed in zooplankton taxonomic diversity do not appear to impact the suite of functional traits present across ecosystems.

Finally, zooplankton diversity did not appear to be reduced by the more intensive human habitat perturbation (mainly via agriculture and urbanization) in the southern regions of the Prairies, Mixedwood Plains and Atlantic Maritimes ecozones, but in all regions low impact sites were explicitly selected (Gibbs *et al.*, 2009; Huot *et al.*, 2019). Thus, at the continental extent, large-scale spatial determinants, related to longitudinal dispersal in our case, appear to be important for zooplankton diversity and distribution (Stoch *et al.*, 2019).

1.5.3 Mechanisms shaping β-diversity

Accounting for taxonomic and functional approaches may be essential in disentangling large scale biogeographical patterns. As expected (Table 1.1), functional overall β-diversity values (0.32) were slightly reduced relative to taxonomic β-diversity (0.47). Greater taxonomic variation across lakes, as observed here is consistent with the literature (Cardoso *et al.*, 2014; Nakamura *et al.*, 2020) independent of the methods used to compute functional β-diversity, and is expected when there is high functional redundancy among sites (Gianuca *et al.*, 2018). Our overall taxonomic β-diversity value is slightly greater than that reported in Winegardner's *et al.* (2017) study of U.S. diatom (0.36); however, their analyses were conducted at the genus level. On the other hand, Soininen *et al.* (2018) found higher average β-diversity (0.62) than ours in their global meta-analysis of species β-diversity studies covering taxa from bacteria to mammals, with latitude emerging as the strongest predictor.

The mechanism shaping total β-diversity in our study was dominated by the richness-difference component (nestedness), regardless of the diversity dimension (taxonomic and functional). This result could be linked to the longitudinal α-diversity patterns that we observed related to geographic dispersal barriers and westerlies as discussed. According to Leprieur *et al*. (2011), a higher richness-difference component of β-diversity can indicate that there has been a large-scale uniform pressure on the territory, such as climate change. Canada is indeed facing intense climate change, at twice global rates, especially in the Prairies, British Columbia and in the North (Warren et Lemmen, 2014; Bush et Lemmen., 2019; Environment and Climate Change Canada, 2019). A strong effect of climate change on zooplankton has previously been detected in western Canada, whereby important association between climate variables and taxonomic or functional composition were detected (Loewen *et al.*, 2019). On the other hand, when taxon-replacement is the dominant mechanism generating β-diversity, variation likely results from strong environmental gradients (Leprieur *et al.*, 2011). Thus, overall, our results point to climate change and important physical barriers to dispersal as key factors shaping zooplankton biogeography. Further exploration of potential mechanisms will come from future LakePulse analyses, wherein we have the opportunity to explore the relative role of local spatial vs. environmental factors, consider food web interactions, as well as quantify changes in sub-fossil assemblages between pre-industrial and contemporary times through sediment core analyses.

In a conservation context, Devictor *et al*. (2010) proposed targeting sites having both high α- and β-diversity values, as a compromise between preserving species-rich sites and ecologically unique sites. Moreover, functional β-diversity is a critical component to consider in conservation planning since functional α-diversity alone does not capture trait uniqueness (Quirino *et al*., 2021). Based on our results, sites from the Boreal Cordillera could be prioritized in management plans, since this ecozone harbors both high α-diversity (eveness, *FDis*) and species and traits LCBD values (see Figure 1.2).

Conservation goals are often focused on individual taxa such as endangered, threatened or keystone species, and in this context, the species contribution to β-diversity (SCBD) metric can be particularly informative. However, most of the zooplankton species in our study that contributed more than the average to taxonomic SCBD (e.g., *Daphnia pulicaria, Bosmina longirostris, Mesocyclops edax*) were also broadly distributed and were not typically found in lakes with significant LCBD. This finding aligns with Vilmi *et al.* (2017) suggestion that considering only SCBD is not sufficient to identify critical sites for conservation, and that it should be combined with other α- and β-diversity values. On the other hand, the species contributing the most to functional SCBD (e.g., *Eubosmina tubicen, Aglaodiaptomus clavipes*) were not all broadly distributed in our study, and could thus be useful candidates for identification of conservation sites. This provides potentially the first evidence that functional traits could be more informative than taxonomy for identifying species contributing the most to β-diversity.

Although this is the first pan-Canadian sampling of zooplankton that adopted a standardized approach over a short 3-year time period and covered 6765 km (longitude) by 2807 km (latitude), some regions of Canada remain poorly represented. In particular, Canada's northernmost ecozones could be more extensively sampled in the future. Eventual inclusion of these northern freshwater zooplankton communities is essential to make further advancements.

1.6 Conclusions

Overall, our study demonstrates the importance of incorporating different spatial scales and diversity dimensions in biogeographical studies. Zooplankton community biomass, composition, α- and β-diversity all varied significantly across regions, but the importance of continental watersheds and of a longitudinal diversity gradient across the Canadian lakes emerged as the stronger trends. By incorporating taxonomic and functional dimensions of β-diversity, we revealed spatial patterns that have not previously been observed, and identified the importance of incorporating functional traits for conservation plans. Future work exploring zooplankton biogeography across Canada including a variety of environmental variables will be essential to disentangle the effects of space from those of land use and climate. Moreover, considering longer-term temporal β-diversity in zooplankton will be key to understand how communities have changed during the Anthropocene, and to predict how they will continue to change in the future.

CHAPITRE 2

ENVIRONMENTAL DRIVERS OF TAXONOMIC AND FUNCTIONAL VARIATION IN ZOOPLANKTON DIVERSITY AND COMPOSITION IN FRESHWATER LAKES ACROSS CANADIAN CONTINENTAL WATERSHEDS

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Cindy Paquette[1,2,3], Irene Gregory-Eaves[2,3] and Beatrix E. Beisner[1,2]

Corresponding author: paquette.cindy@courrier.uqam.ca

[1]Department of Biological Sciences, University of Quebec at Montreal, Montreal, Quebec, Canada;

[2]Interuniversity Research Group in Limnology (Groupe de recherche interuniversitaire en limnologie; GRIL);

[3]Department of Biology, McGill University, Montreal, Quebec, Canada

2.1 Abstract

Canada is home to more lakes than any other nation, but there is a fragmented and limited understanding of the ecological status of these water bodies. Zooplankton are excellent bioindicators of lake health, given their central food web position. To date, many studies have investigated the effect of individual stressors on zooplankton communities, mediated through changes in water quality (e.g., macronutrients, temperature, or chemicals). Increasingly, stressors act simultaneously in lakes, often over extended periods of time. As part of the NSERC Canadian Lake Pulse Network project, pelagic zooplankton were sampled in 624 lakes across Canada, spanning six continental drainage basins. We evaluated the effect of 40+ environmental variables on zooplankton diversity and community composition, considering both taxonomic and functional approaches. We also tested specific hypotheses on the relationships between zooplankton communities and environmental conditions, including eutrophication, calcium, chloride and fish predation. We found that lake morphometry variables were among the most important predictors of zooplankton diversity, while water quality metrics were more critical in explaining variation in community composition. Our results also reveal significant heterogeneity across Canada, with contrasting effects of environmental drivers among continental watersheds, highlighting that response models cannot be assumed to apply universally.

2.2 Introduction

Freshwater is essential to humanity as it provides us with drinking water and nourishment, but also many other ecosystem services that we depend upon. Inland water is used for agriculture, fisheries, recreation, tourism, and many other social and economic activities. Freshwater ecosystems are also hotspots for diversity when compared to terrestrial systems (Strayer et Dudgeon, 2010) and also an integral part of global biogeochemical cycles (Tranvik *et al.*, 2018). However, anthropogenic activities can influence and threaten freshwater resources, which in turn can alter the ecosystem services they provide. Intensive agriculture (Ribaudo et Johansson, 2007), urbanisation and related road salt application (Dugan *et al.*, 2017), fisheries overexploitation (Reid *et al.*, 2000), exotic species introduction (Ricciardi et MacIsaac, 2011), climate change (Schindler, 2009), and eutrophication arising from multiple causes (Smith et Schindler, 2009) are all stressors leading to the disturbance of lacustrine environments. With this growing number of concomitant stressors altering the functioning of freshwater lakes, detection of early signals of change in lakes are needed, before lake ecological functions and services change further.

Zooplankton communities, central to lake food webs are excellent indicators of water quality and lake functioning, especially when considering functional trait composition, which can be more directly related to the mechanisms driving some ecosystem functions (Hébert *et al.*, 2017). Pelagic crustacean zooplankton are considered to be key indicators of recent changes in lakes because, owing to their short generation times, they respond quickly to disturbances and can thus provide early detection of wider ecosystem shifts or at least track environmental changes (Carvalho *et al.*, 2013; Khalifa *et al.*, 2015). Because of their central position in the food web, changes in zooplankton diversity could be critical to whole lake ecosystem functioning. Moreover, crustacean zooplankton diversity can be used to estimate quantitatively community variability among lakes and to monitor ecosystem changes related to environmental disturbances. Various studies have demonstrated responses by zooplankton communities to stressors including: eutrophication (Jeppesen *et al.*, 2011), pH (Couture *et al.*, 2021; Havens *et al.*, 1993), salinity (reviewed in Hintz et Relyea, 2019), water level (Nevalainen *et al.*, 2011), toxic substances (reviewed in Pashkova, 2013) and calcium declines (Jeziorski *et al.*, 2008; Palmer *et al.*, 2011).

The interactive effects of water quality stressors, including climate change, are not well understood, especially under natural conditions (Jackson *et al.*, 2016; Titeux *et al.*, 2016). Over the years, many studies have investigated the effect of individual stressors on zooplankton communities, mediated through changes in water quality (e.g., macronutrients, temperature, or chemicals). Increasingly, however, stressors act simultaneously in lakes, sometimes over extended periods of time. For instance, changes in pH can interact with other factors such as predation pressure, total phosphorus and dissolved organic carbon concentrations (Korhola and Rautio, 2001; Yan *et al.*, 2008). Moreover, beyond considering only in-lake water properties, it is important to relate changes in lake communities to human activities in their adjacent watersheds, because land use and water quality are strongly correlated (e.g. , Lee *et al.*, 2009) and are also an important consideration for zooplankton community composition (Dodson *et al.*, 2005).

This study is one component of the NSERC Canadian Lake Pulse Network, the goal of which is to evaluate the national health status of freshwater lakes by assessing how they have changed since pre-industrial times and determine how they will continue to change in the future (Huot *et al.*, 2019). Worldwide, Canada is the country with the largest number of lakes (Messager *et al.*, 2016), but there has been no systematic evaluation of the health of these lakes despite their importance in term of drinking water, agriculture and recreational tourism, among others. LakePulse provides a unique and novel opportunity to explore freshwater communities across north temperate to subarctic continental environmental gradients from protists to phytoplankton and bacteria (Kraemer *et al.*, 2020; MacKeigan *et al.*, 2022) to multi-trophic assemblages (Griffiths *et al.*, 2021).

In addition to the influence of environmental factors, spatial proximity can influence lake zooplankton community structure through dispersal (e.g., Beisner *et al.* 2006; Rocha *et al.* 2020). Recently, we examined biogeographical patterns in the LakePulse cross-Canada crustacean zooplankton communities, independently of environmental factors (Paquette *et al.*, 2021). In that study, we demonstrated the presence of important geographical gradients related to longitudinal dispersal limitation. Our goal in this current study is to focus on the environmental drivers rather than dispersal-related processes. To this end, crustacean zooplankton communities across hundreds of lakes were analysed using taxonomic and functional trait approaches to determine how diversity and community composition at this continental-scale is influenced by local environmental factors, lake morphometry, and watershed land use. We also explored whether variation in diversity and community composition were influenced by fish predation metrics and quantified the relative importance of fish variables with respect with water quality indicators, lake morphometry, and land use. Moreover, one advantage of the continental sampling carried out by LakePulse is that we have very large gradients allowing us to test specific hypotheses regarding zooplankton ecology. Based on recent identification of critical stressors for zooplankton in north temperate lakes, we hypothesized that zooplankton taxonomic diversity would be reduced in lakes with (a) lower calcium concentrations (Jeziorski *et al.*, 2008) and (b) higher salinity, related to road salt application (Arnott *et al.*, 2020). In relation to eutrophication, we evaluated productivity-diversity relationships and expected (c) to observe a curvilinear pattern between taxonomic diversity and total phosphorus (Barnett et Beisner, 2007). We also wanted to test the common diversity-habitat size relationship (e.g., Gaston, 2000) and hypothesized (d) that larger and deeper lakes would support greater taxonomic and functional diversity. Finally, because fish predation has been demonstrated to control zooplankton composition (Brooks et Dodson, 1965; Jeppesen *et al.*, 1997), we hypothesized that when included, (e) fish metrics would be the most important drivers of community structure. Because of the extremely large environmental gradients at this continental scale, we report on differences in environmental filtering processes among continental drainage basins representing large-scale watersheds. While the effect of multiple factors on zooplankton communities has previously been examined (e.g., Pinel-Alloul *et al.* 1995; Macleod *et al.* 2018; Couture *et al.* 2021), ours is the first standardized assessment that considers the combined effect of in-lake factors, land use, and fish predation on zooplankton taxonomic and functional diversity at the continental scale, providing the most comprehensive understanding of the environmental drivers of lake crustacean zooplankton diversity and compositional variation.

2.3 Material and methods

2.3.1 Lake sampling

As part of the NSERC Canadian Lake Pulse Network, 664 lakes across Canada were each sampled once mid-summer (July-August) in one of three years (2017-2019). Lakes were selected randomly among all lakes located no further than 1 km from road access, within a stratified design to ensure representation across ecozones, lake area and human land use impact (see Huot *et al.*, 2019). The lakes sampled covered six ocean drainage areas (continental basins): Pacific Ocean, Arctic Ocean, Hudson Bay, Gulf of Mexico, Great Lakes-St. Lawrence and Atlantic Ocean, as delineated by the Canadian National Hydrographic Network.

Environmental variables collected for each lake included lake morphometry, water quality and land use data. Lake morphometry variables were lake depth, lake area, stratification status and watershed area, as well as data on lake circularity, discharge, residence time, and watershed slope, obtained from HydroLAKES v. 1.0 (Messager *et al.*, 2016). Water quality variables, characterized by water physical and chemical properties, were collected or measured at the deepest point of each lake by all LakePulse team members. Secchi depth and physico-chemical measurements (temperature, pH, specific conductivity, salinity, dissolved oxygen (DO), water pressure, and in vivo chlorophyll-*a* (chl*a*) fluorescence) were performed on site (field protocols described in NSERC Canadian Lake Pulse Network, 2021). Surface water was collected with an acid-washed integrated tube sampler from surface to twice the secchi depth, to a maximum of 2 m depth (hereafter: tube sample). In thermally-stratified lakes, hypolimnetic water was collected using a cleaned van Dorn bottle at 1 m above the sediment surface (bottom sample). Lake water was stored in the dark in icepack-chilled coolers until further processing (later in the day) and was subsampled for lake colour, extracted chl*a*, organic and suspended mineral sediments (SPM), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), nitrite-nitrogen (NO_2^--N), nitrate-nitrogen (NO_3^--N), TN:TP ratio, calcium (Ca^{2+}), potassium (K^+), sodium (Na^+), chloride (Cl^-), magnesium (Mg^{2+}) and sulfate (SO_4^{2-}). Finally, the land use types (urban, mines, agriculture, pasture, forestry and managed grassland), and the fractions of water versus natural landscape were also characterized for each lake watershed, as described by Huot *et al.* (2019). The full set of environmental variables, their abbreviations, sampling and analyses summaries are listed in Table 2.1.

Integrated water column crustacean zooplankton samples were collected at the sampling location in each lake using a 100µm mesh Wisconsin net. Samples were preserved in 70% (final concentration) ethanol after an initial CO_2 narcotization, and stored at room temperature until identification to species and biomasses estimations using measured individual length and established size and weight relationships for each species by BSA Environmental Services (Ohio, U.S.A.). For additional details on zooplankton sampling and identification, see Paquette *et al*. (2021). Our final dataset included 624 lakes (Figure 2.1) for which zooplankton reached the minimal count of 100 individuals total.

2.3.2 Fish sampling

In a subset of 314 lakes (Figure 2.1), fish data was collected as part of the FishHab project (fishab.weebly.com; B.E. Beisner pers.comm.), using data provided by Canadian provincial and territorial governments. Because sampling methods varied greatly among regional datasets, only presence data was used. Three fish community metrics were estimated for each lake: maximum trophic level (maxTL), piscivore richness, and planktivore richness. Fish trophic position by species were obtained using FishBase (https://www.fishbase.se/), and the highest trophic level for each lake (a value between 2.0 and 5.0; maxTL) was recorded as a quantitative index. Fish species were then assigned a trophic position of piscivore (trophic level or TL > 3.5) or planktivore (TL ≤ 3.5) based on FishBase classification of known planktivore and piscivore species (adult stages). The total number of piscivore and planktivore taxa were then recorded for each lake, as in Fu *et al.* (2021).

Table 2.1 Variables measured, abbreviations, units, transformations applied, and sample depth of environmental variables.

Variable	Abbreviation	unit	Transfor-mation	Sample depth[1]	Selected VIF[2]
Morphometry					
Lake area	area	km2	log	-	yes
Lake depth	depth	m	log	-	yes
Circularity	-	-	sqrt	-	yes
Stratification	-	Y/N	none	-	yes
Discharge	-	m^3/sec	log	-	no
Residence time	res_time	days	log	-	yes
Watershed area	wshd_area	km2	log	-	yes
Mean slope in watershed	mean_slope	°	log	-	yes
Slope 100m	-	°	log	-	yes
Water quality					
Chlorophyll *a* – in vivo fluorescence	chl*a*_tube chl*a*_bottom	µg/L	log	Tube, bottom	yes
Chlorophyll *a* – filtration	chl*a*	µg/L	log	Tube	yes
pH	-	-	none	Epi, hypo	yes
Conductivity	-	mS/cm	-	Tube, hypo	no
Salinity	-	PSU	log	Tube, hypo	hypo
Temperature	T° Temp_epi Temp_hypo	°C	none	Top0.5m, top1m, mean epi, mean water column, mean hypolimnion	Epi, hypo
Water pressure	-	decibar	-	Tube, bottom	no
Dissolved oxygen	DO	%; (mg/L)	none	Tube, bottom	% Top, Bottom
Color	-	mg/L Pt	log	Tube	yes
Secchi	-	m	log	-	yes
Organic and suspended mineral sediments	SPM	mg/L	log	Tube	yes
Dissolved organic carbon	DOC	mg/L	log	Tube	yes
Dissolved inorganic carbon	DIC	mg/L	log	Tube	yes
Total phosphorus	TP	ug/L	log	Tube, bottom	Bottom
Soluble reactive phosphorus	SRP	ug/L	log	Tube, bottom	yes

Table 2.1 Continued

Variable	Abbreviation	unit	Transfor-mation	Sample depth[1]	Selected VIF[2]
Total nitrogen	TN	mg/L	log	Tube, bottom	yes
Nitrite-nitrogen	NO_2^--N	µg/L	log	Tube, bottom	yes
Nitrate-nitrogen	NO_3^--N	µg/L	log	Tube, bottom	yes
Total nitrogen: total phosphorus ratio	TN:TP ratio	-	log	Tube	yes
Calcium	Ca^{2+}	mg/L	sqrt	Tube	yes
Potassium	K^+	mg/L	log	Tube	yes
Sodium	Na^+	mg/L	log	Tube	yes
Chloride	Cl^-	mg/L	log	Tube	yes
Magnesium	Mg^{2+}	mg/L	-	Tube	no
Sulfate	SO_4^{2-}	mg/L	log	Tube	yes
Land use					
Agriculture	-	%	log	-	yes
Forestry	-	%	log	-	yes
Grassland	-	%	log	-	yes
Mines	-	%	log	-	yes
Natural landscapes	natlandscapes	%	sqrt	-	yes
Pasture	-	%	log	-	yes
Urban	-	%	log	-	yes
Water	-	%	log	-	yes
Fish (n=314 lakes)					
Maximum trophic level	maxTL	-	none	-	yes
Piscivore richness	-	# species	sqrt	-	yes
Planktivore richness	-	# species	sqrt	-	yes

[1] The tube sample was collected from the surface to twice secchi depth (to a maximum of 2 m depth), and the bottom sample was collected at 1 m above surface sediments. Epilimnetic and hypolimnetic variables correspond to the mean value across the length of the epilimnion and hypolimnion, respectively, as estimated based on the lake thermal profile.

[2] Indicates whether the variable was retained (yes or name of selected variable depth for multiple depths) or eliminated (no) following VIF selection. The full set of variables was used in the URTs, while the reduced data set (only "Selected VIF" variables) was used in the PCA, RFs, GAMMs, and variation partitioning.

2.3.3 Statistical analyses

All statistical analyses were performed in R v. 4.1.0 (R Core Team, 2021). In the continental basin scale analyses, the Gulf of Mexico (n=2) and Hudson Bay (n=145) basins were combined based on species and traits similarity, in order to balance continental basin observational group sizes (as in Paquette *et al.*, 2021).

2.3.3.1 α-diversity estimation

Crustacean zooplankton taxonomic composition and associated biomass was used to estimate species richness, Shannon entropy, Simpson diversity and Pielou's evenness using *diversity()* in the vegan R-package (Oksanen *et al.*, 2019). Rarefied richness was also estimated by randomly subsampling species counts to the lowest count size (109 individuals) using *rarefy().* Functional diversity was estimated using functionally classed species-specific traits from the literature (Barnett *et al.*, 2007; Demott et Kerfoot, 1982; Griffiths *et al.*, 2019). The traits used were resource acquisition, habitat, trophic group and size (see Paquette *et al.,* 2021 for trait database). Functional evenness (*FEve*; Villéger *et al*., 2008), functional dispersion (FDis; Laliberté et Legendre, 2010) and functional richness (FRic; Villéger *et al.*, 2008) were estimated using all traits in the *dbFD()* function (FD R-package) with Gower distances (Laliberté *et al.*, 2014).

2.3.3.2 Data visualization - PCA ordination

To visualize the relations between the environmental variables and the diversity indices, a correlation-based principal component analysis (PCA) was performed using the scaled environmental data from the 624 lake sites using the vegan package (Oksanen *et al.*, 2019). Taxonomic and functional diversity indices were then added passively to the PCA using *predict()*. Prior to the ordination, environmental variables were transformed by either square root, or $\log_{10}$ transformation, to render the distribution of each variable closer to normality (Table 2.1). Missing morphometric and hypolimnetic (or bottom) data were replaced by ecozone means, while missing epilimnetic (or tube sample) chemistry data was imputed using the *missForest()* function (Stekhoven et Bühlmann, 2012). To reduce the variable list and remove colinear variables, variation inflation factor (VIF) analysis was performed on the morphometry and water quality data, using *vifstep()* function in the usdm package (Naimi *et al.*, 2014) with a correlation threshold of 10. Transformations and variables retained are identified in Table 2.1.

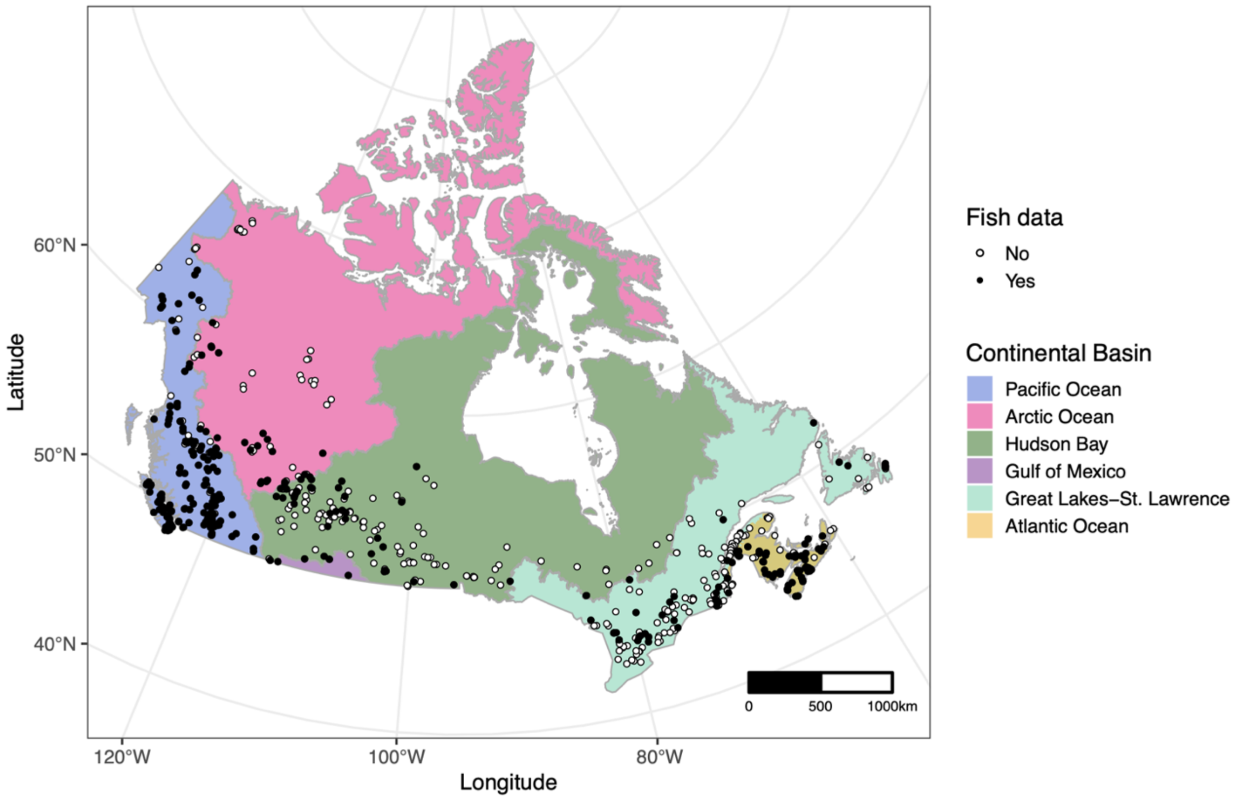

Figure 2.1 Map of lakes sampled by the NSERC Canadian Lake Pulse Network for pelagic zooplankton (n = 624). Lakes are contoured by the differently colored continental basins with filled black dots indicating the presence of fish data. The map was created using Canada Atlas Lambert projection (NAD83 CSRS).

2.3.3.3 Identifying environmental thresholds for diversity

Univariate regression trees (URTs) were used to constrain zooplankton taxonomic and functional diversity indices by the environmental variables. This method allows the partitioning of sampling sites (lakes) through the identification of thresholds in the explanatory variables using the full set of untransformed environmental variables. URTs were computed with the R package mvpart (Therneau et Atkinson, 2014), using 10 cross-validation groups and 100 iterations. The best trees were selected, i.e. trees with the lowest cross-validation errors (Borcard *et al.*, 2018). The URT analyses were conducted both on the full set of lakes (n=624) and on the subset of lakes containing fish data (n=314), where fish variables (maxTL, planktivore richness and piscivore richness) were included as explanatory variables. The regression trees were also performed separately for each continental basin to account for the extremely large gradient in many environmental variables at this continental scale. R^2 barplots were produced to visualize the fit of each continental basin and diversity index.

2.3.3.4 Non-linear modelling of diversity

To model diversity indices as a function of environmental factors, we used a combination of random forest (RF) classification and general additive mixed models (GAMMs). RF consists of a large number of decision trees that operate together as an algorithm, acting as a powerful screening tool to analyze large and complex ecological data while remaining robust to the inclusion of low importance variables (Fox *et al.*, 2017). We computed country-wide RF models on taxonomic and functional diversity indices, with the same normalized-reduced environmental dataset used in the PCA. We ran the models using both the full lake set and on the reduced lake set with associated fish data, where fish metrics were added as potential explanatory variables. The RF algorithms were performed using *cforest()* function in the party package (Hothorn *et al.*, 2021) utilizing conditional inference trees. The conditional approach of R package permimp (Debeer *et al.*, 2021) was used to evaluate variable importance.

For each RF model produced, the ten most important predictors of each model were added as fixed smooth terms to a generalized additive mixed model (GAMM) to assess specific inputs of environment variables on diversity. GAMMs were computed with mgcv R package (Wood, 2021), using restricted maximum likelihood (REML) as smoothing parameter estimation method and the continental basins as random smooth factors. The random smooth factor includes the random intercept and slope implicitly, but also allows the general slope of each splines to vary in a non-linear way for each continental basin level. GAMM plots were produced with the *plot_smooth()* function of itsadug package (Van Rij *et al.*, 2020) for each diversity indices.

2.3.3.5 Factors affecting variation in community composition

To compare the main types of factors (lake morphometry, water quality and land use) influencing variation in zooplankton taxonomic and functional community composition, we conducted 3-way variation partitioning analyses across all Canadian lakes together and by continental basin regions. Variance partitioning was done separately on zooplankton species or functional trait biomass data (Hellinger-transformed). Normalized and evaluated for collinearity, environmental variables of each fraction were forward-selected separately prior to the variation partitioning, conducted with the *varpart()* function in vegan package (Oksanen *et al.*, 2019). The full set of forward-selected variables were then included in redundancy analyses (RDAs) to explore the relationships between the Hellinger-transformed biomass of zooplankton taxa or traits and the environmental dataset.

To evaluate the specific effects of fish metrics relative to morphometry, water quality and land use variables, we conducted 4-way variation partitioning analyses for the 314 lakes with fish and zooplankton data across Canada and by continental basin. This method allowed us to quantify the variation in zooplankton composition explained by fish variables, while controlling for the effects of the other environmental variable fractions (Borcard *et al.*, 2018). As for the 3-way partitioning, analyses were done separately on the zooplankton species and functional trait biomasses, and RDAs were performed between the full forward-selected environmental data set and zooplankton species or traits.

2.4 Results

2.4.1 Environmental variability among lakes and zooplankton diversity

A principal component analysis (PCA) revealed spatial patterns in zooplankton taxonomic or functional diversity and the environmental data. PC1 and PC2 explained 29.4 and 9.3% of variance in the environmental data respectively (Figure 2.2). On the first PCA axis, lakes set in watersheds with extensive agriculture and pasture were associated with high nutrient and ion levels (TN, SRP, Na, K, Cl) and higher DIC and DOC concentrations. These lakes were mostly located in the Hudson Bay continental basin, and were diametrically opposed to deep transparent lakes located in more natural watersheds in all the other continental basins. On the second axis, the deeper and larger lakes mostly from the Pacific Ocean basin plotted against highly coloured lakes with high chl*a* concentrations and greater epilimnetic and hypolimnetic temperatures from a variety of continental basins, the most extreme of which occurred in the Atlantic Ocean basin at the other end of the country. Passively added taxonomic diversity indices all plotted positively along the first PCA axis and were associated with lakes from natural and forested landscapes, and linked with low ion and nutrient concentrations. Functional dispersion (*FDis*) and functional evenness (*FEve*) also plotted similarly, close to deep transparent lakes. The exception was functional richness (*FRic*), which was associated with ion- and nutrient-rich sites where pasture and agriculture are the main land-use types.

2.4.2 Identifying environmental thresholds for diversity

Taxonomic and functional diversity indices were associated with a variety of environmental gradients, revealed by the univariate regression trees (URTs). Across Canada, evenness (R^2=0.58), Simpson diversity (R^2=0.54), Shannon diversity (R^2=0.50) and *FDis* (R^2=0.56) had the highest percentages of variance explained and all highlighted the importance of morphometry variables (gray bars in Figure 2.3). The first split in the URT on Shannon diversity divided the sites across Canada by lake circularity, with greater diversity observed in more irregularly shaped lakes (circularity < 0.11). Maximum lake depth commonly determined the first split in the URTs on evenness, Simpson diversity and *FDis*. Greater diversities were consistently found in lakes where the maximum depth was ≥20.5.

At the continental basin level (colored bars in Figure 2.3), the highest variance explained (R^2=0.87) overall was reached with *FRic* in the Atlantic Ocean basin, where 75.05 mg/L of chloride separated 6 lakes with high *FRic* from those of lower *FRic*. However, it should be noted that the URT with its four selected variables could only split 25 lakes out of the total of 91 lakes in the Atlantic Ocean basin, likely because of missing values. In the Arctic Ocean basin, colour, DOC or pH (often interrelated) were selected as the primary variable explaining thresholds in diversity metrics. Overall, morphometry (lake depth and circularity) or physical variables (pH, DO, water pressure and temperature), were often the determinants of the first split of the most powerful URTs (those with R^2>0.375; Figure 2.3). The full country-wide and within continental basin URT error table and plots are shown in Annexe H.

Finally, in the subset of 314 lakes where fish presence data was documented, explanatory fish variables (maxTL, piscivore and planktivore richness) were never selected in the country-wide, nor within any of the continental basins URTs (results not shown).

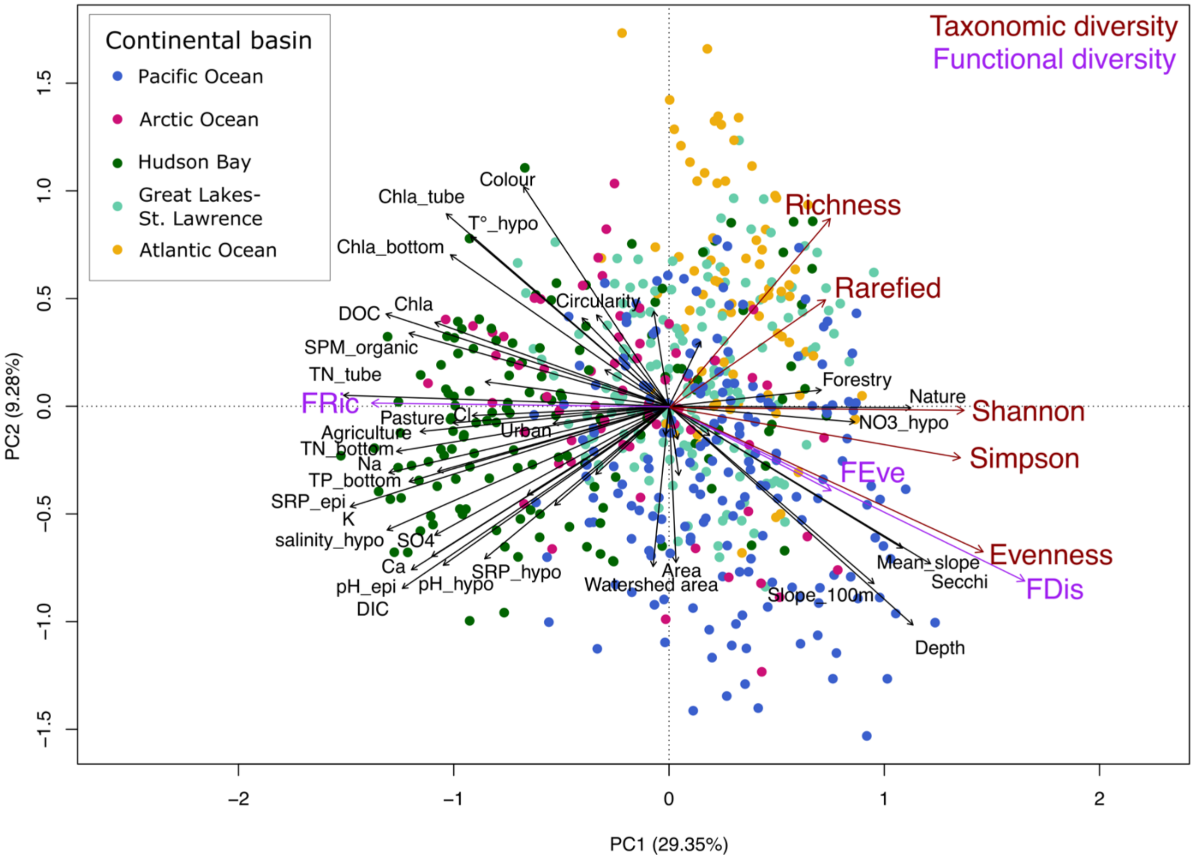

Figure 2.2 PCA on environmental variables (scaling 2) for the 624 sites (circles), colored by continental basin (listed from west to east) as in Fig. 1. Taxonomic and functional diversity indices were added passively. The percent of the site variance explained is displayed next to each of the PCA axes.

2.4.3 Drivers of zooplankton diversity using GAMMs

We also fit generalized additive mixed models (GAMMs) to more fully explore the non-linear effects of environmental variables on taxonomic and functional diversity to evaluate how these relationships differed among continental basins. Using random forest (RF) models to select predictors for the GAMM models, we found that morphometric variables (i.e., circularity and lake area) were classified as the variable of greatest importance for 6 of the 8 diversity indices. R^2 in the RF models varied from 0.01 (*FEve*) to 0.27 (rarefied richness; see all RF conditional permutation importance R^2 and plots in Annexe I). The fitted GAMMs revealed important variation among continental basins for all diversity indices besides *FEve* (Table 2.2).

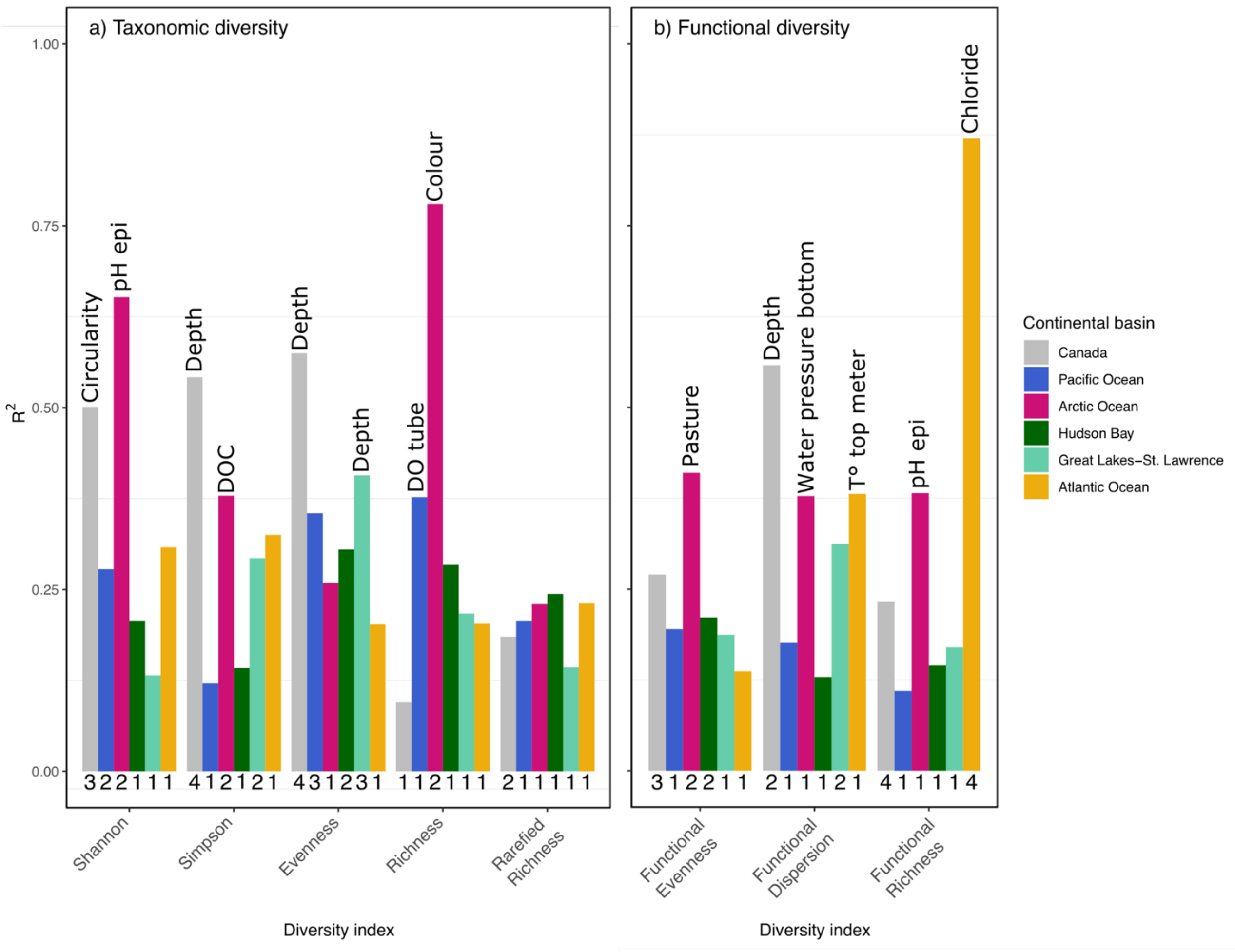

Figure 2.3 Barplots of taxonomic (a) and functional (b) diversity index URT R^2 across all Canadian lakes and grouped by continental basin. Trees with the lowest cross-validated error were selected. Numbers below the bars represent the number of variables that were selected in each tree. Written above the bars are the first variables selected in those plots for which $R^2 > 0.375$.

The GAMM for taxonomic richness had the greatest predictive power ($R^2 = 0.41$; 48.2% deviance explained). Among the variables selected from the country-wide taxonomic richness RF (see Supporting Information Annexe I), circularity, epilimnetic temperature, lake area, watershed area, hypolimnetic TP, mean slope, sodium, hypolimnetic pH and water colour, with sodium having the greatest predictive power (p=1.75e-06) (Table 2.2; Figure 2.4). Many variables showed contrasting responses among continental basins. For instance, taxonomic richness increased along the sodium gradient in the Arctic region, while there was a negative relationship in the

Hudson Bay region. GAMM plots for top RF predictors for all diversity indices can be visualised in Supporting Information Annexe J.

Table 2.2 Taxonomic and functional diversity indices along with the R^2 and percentage of deviance explained (separated by -) and variable of greatest importance with respective p-values in parentheses from the general additive mixed models (GAMMs). The greatest value across all diversity indices is highlighted in bold.

Diversity index	**R^2 - % deviance explained**	**Variable of greatest importance (*p*-value)**
Shannon	0.21 - 25.7%	Max depth (1.49e-05)
Simpson	0.14 - 18.4%	Lake area (5.16e-05)
Evenness	0.11 - 15.3%	TN bottom (5.66e-05)
Richness	**0.41 - 48.2%**	Sodium (1.75e-06)
Rarefied Richness	0.36 - 42.9%	Sodium, Circularity (2e-16)
Functional Evenness	0.01- 1.68%	NA
Functional dispersion	0.22 - 28.1%	Max depth (2e-16)
Functional richness	0.23 - 26.5%	Chloride (8.9e-07)

From the reduced 314 lake dataset, fish explanatory variables were selected in the RF models for all diversity indices, with the exception of *FEve* (see all RF R^2 table and conditional permutation importance plots for the 314 lakes analysed together across Canada in Annexe K). Planktivore richness was significant in the GAMM models for *FRic*, rarefied richness and taxonomic richness, with a general pattern of higher diversity with increased planktivore richness. The maximum trophic level was also significant for Shannon diversity, but we observed opposing trends among continental basins (Figure 2.5; see all GAMM plots for top RF predictors of reduced 314 lakes in Annexe L).

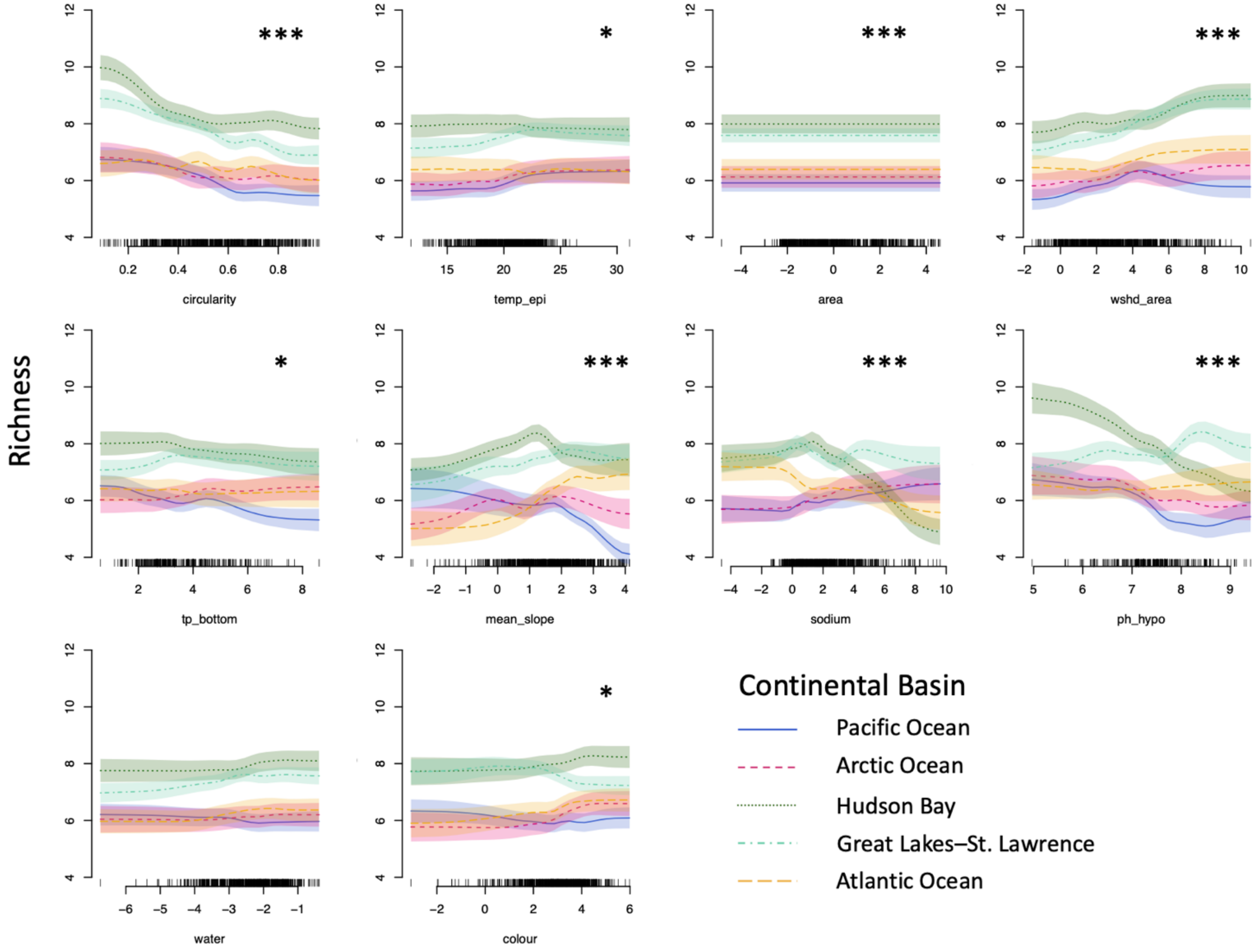

Figure 2.4 GAMM plots of fitted taxonomic richness values against the 10 most important predictors as sorted by RF model, with continental basins as random smooth factor. Shaded area represents the confidence interval, reduced at SE = 0.5 to aid visualization. Full variables names and transformations are found in Table 1. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

2.4.4 Environmental and biotic predictors of zooplankton structure

Using variation partitioning, we compared the relative influence of lake morphometry, water quality and land use variable groupings on zooplankton taxonomic and functional community composition. Across all Canadian lakes, our predictors explained 16.9% and 15.2% of the variation in taxonomic and functional composition, respectively (Table 2.3). In both models, water quality variables were the most important drivers, alone explaining 8.6% of changes in zooplankton species and functional traits (excluding that shared with other fractions). We observed the same pattern in the analyses done at the continental basin scale for species and traits, with water quality variables being the most important in all regions; the exception was in the Atlantic Ocean basin where morphometry variables explained the highest fraction of compositional change.

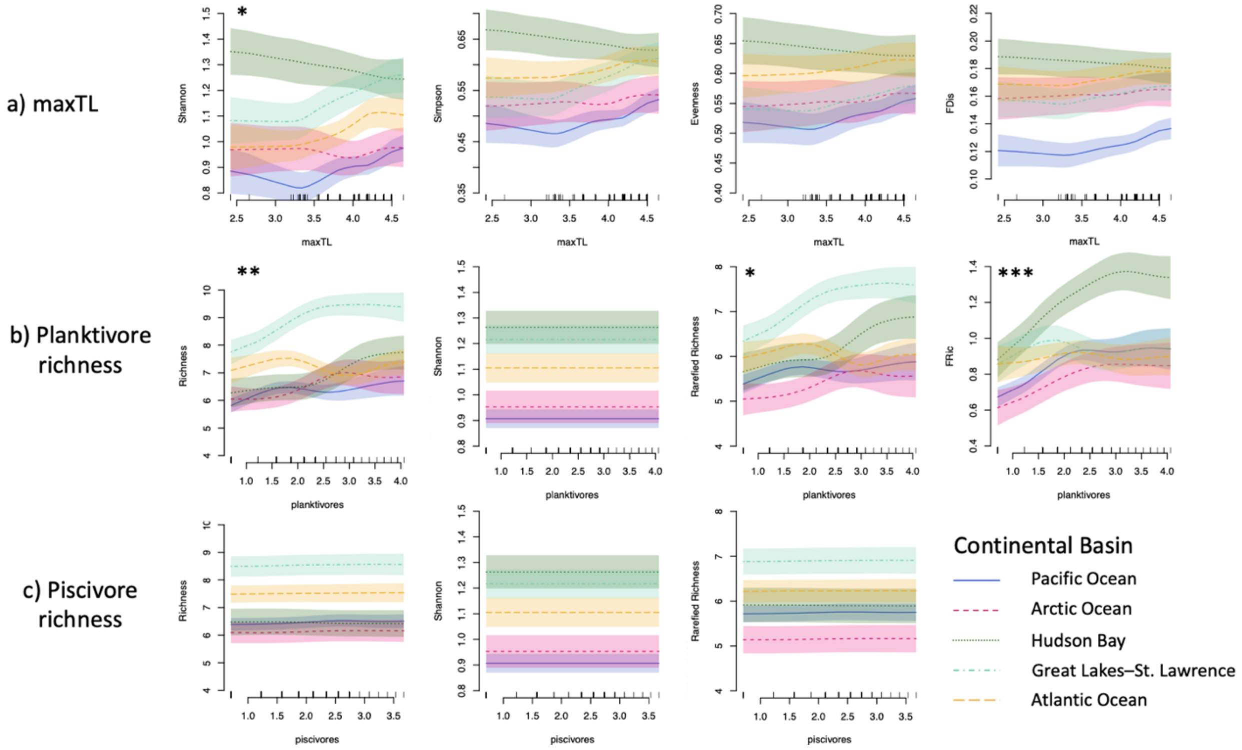

Figure 2.5 GAMM plots of fitted taxonomic and functional diversity indices against maxTL (a), planktivore richness (b), and piscivore richness (c). Plots where fish variables were selected among the 10 most important predictors as sorted by the RF models are shown, with continental basins as random smooth factor. Shaded area represents the confidence interval, reduced at SE = 0.5 to help visualization. Fish metric transformations can be found in Table 2.1. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

RDAs were then performed to relate species or traits to the environmental gradients. In the RDA on the taxonomic species data (R^2_{adj} =0.17, *p*=0.001), axes 1 and 2 explained 8.4% and 2.6% of variation respectively. SRP in the hypolimnion, potassium and DIC were identified as most important predictors (axis 1), while the epilimnetic temperature and the watershed pasture fraction loaded positively on axis 2. *Daphnia pulicaria* was more prevalent in high nutrient and ion concentration sites, with most other species showing the opposite pattern (Figure N.1a in Annexe N). The RDA on the functional traits resulted in a significant model (R^2_{adj} =0.16, *p*=0.001) with the first two significant axes accounting for 7.4% and 3.9% of variation respectively. SRP in the hypolimnion loaded strongly on the first RDA axis, along with the D-filtration feeding mode in opposition to the B-filtration feeding mode and small taxa. The second axis was primarily a depth gradient (Figure N.1b in Annexe N).

We also calculated the effects of fish variables on zooplankton taxonomic and functional community composition, relative to the effects of lake morphometry, land use and water quality variable types. The total variation explained in the taxonomic and functional composition models was 18.3% and 15.0%, respectively (Table 2.3). Again, water quality variables were the most important for changes in taxonomic and functional composition, explaining 8.7% and 8.2% of variation, respectively. Forward-selected fish variables explained the lowest fraction of variation in the zooplankton species (0.6%) and functional traits (0.5%). Fish variables did not emerge as significant predictors of taxonomic composition when running the 4-way variation partitioning by continental basins, and explained a significant, but low fraction (1.6%) of trait variation in the Pacific Ocean basin (data not shown). RDA using taxonomic composition and forward-selected environmental variables revealed a significant model (R^2_{adj} =0.18, p=0.001), with the first two axes explaining 9.0% and 3.7% of variation, respectively. In relation to fish, *Bosmina longirostris* and *Mesocyclops edax* were more prevalent in lakes with a greater planktivore fish richness, lower SRP concentrations (hypolimnion), and greater DO % near the lake bottom (axis 1). Along axis 2, *Diacyclops thomasi* was associated with greater piscivore richness, lake maximum depth and mean slope (Figure N.2a in Annexe N). Overall, the omnivore-carnivore trophic group and the raptorial feeding types were more prevalent in larger (area) lakes with higher planktivore fish richness in the RDA on functional composition (R^2_{adj} =0.15, p=0.001; axes 1 and 2 = 8.1 % and 4.6 % of variation respectively; Figure N.2b in Annexe N).

2.5 Discussion

Our study investigated zooplankton diversity relationships and compositional variation across Canada using the first standardized national survey of Canadian lakes covering a broad range of environmental factors (Huot *et al.*, 2019). Combining a suite of taxonomic and functional diversity metrics, with more than 40 environmental variables across 624 lakes, our study explores environmental, land use and morphometric drivers of zooplankton diversity and assemblages.

Overall, we were able to relate up to 48.2% deviance in zooplankton diversity to environmental factors.

Table 2.3 Variation partitioning table for total variance explained, as well as lake morphometry, water quality, land use and fish pure effects for zooplankton taxonomic (a) and functional trait (b) community compositions for the 314 lakes with fish data, across all 624 Canadian lakes, and by continental basin. The variation explained by shared fractions is reported in Annexe M.

a) Species	**Variation explained**	**Morphometry**	**Water quality**	**Land use**	**Fish**
Reduced fish data set	0.181	0.009	**0.086**	0.012	0.006
Canada	0.169	0.011	**0.087**	0.015	**-**
Pacific Ocean	0.186	0.011	**0.074**	0.037	-
Arctic Ocean	0.148	0.003	**0.054**	-0.007	-
Hudson Bay	0.218	0.010	**0.106**	0.024	-
Great Lakes-St.Lawrence	0.160	0.027	**0.069**	0.0001	-
Atlantic Ocean	0.178	**0.044**	0.036	0.024	-

b) Traits	**Variation explained**	**Morphometry**	**Water quality**	**Land use**	**Fish**
Reduced fish data set	15.0	0.009	**0.082**	0.012	0.05
Canada	0.158	0.018	**0.077**	0.015	-
Pacific Ocean	0.175	0.020	**0.061**	0.030	-
Arctic Ocean	0.147	0.026	**0.085**	0.013	-
Hudson Bay	0.224	0.011	**0.192**	NA	-
Great Lakes-St.Lawrence	0.188	0.026	**0.062**	0.004	
Atlantic Ocean	0.164	**0.089**	-0.008	0.011	-

Furthermore, we observed that country wide, morphometry was the most important correlate of zooplankton diversity, while water quality and land use variables played contrasting roles among continental watersheds, revealing spatial patterns that have not previously been observed. However, water quality variables explained the greatest amount of variation in zooplankton when exploring community composition, while surprisingly, fish-associated variables explained almost none. We found only weak/moderate support for most of our literature-based hypotheses, with contrasting patterns between regions, challenging generalized application of results from smaller-scale studies.

2.5.1 Zooplankton response to lake morphometry

Overall, zooplankton diversity across Canada was best explained by lake morphometry variables, including lake depth, area and circularity. In general, we observed greater diversity values in large, deep and irregular-shaped lakes. We also identified a threshold of 20.5m depth for high diversity across Canadian lakes, contrasting with the 8m depth threshold for greater richness previously established in Precambrian Shield lakes (Keller et Conlon, 1994). It is well known that larger ecosystems can maintain greater diversity (Gaston, 2000). While some exceptions to this pattern occur (Hessen *et al.*, 2006), most studies of zooplankton taxonomic diversity show a positive relation with lake size or depth, where greater spatial horizontal and vertical niche differentiation is possible (Browne, 1981; O'Brien *et al.*, 2004; Strom, 1946). Moreover, larger and deeper lakes harbor longer food chains (Post *et al.*, 2000) and thereby, greater piscivore biomasses could ease selective predation on zooplankton by planktivorous fish and favor diversity. While piscivore richness and lake depth did plot closely in our RDA analyses, we did not observe significant effects of piscivore richness on zooplankton diversity. It is possible that adult piscivore richness is not the best metric of actual or perceived predation pressure at this trophic level, and thus does not accurately capture the cascading effects on zooplankton. Data on fish abundances or biomasses would surely provide better metrics of predation pressure in our lakes.

Interestingly, an effect of fish predation could be indicated by response to lake shape with an observed negative non-linear relationship between zooplankton richness and lake circularity (Figure 2.4). Piscivorous fish in circular lakes appear to be more omnivorous than in reticulate lakes, where they feed more exclusively on planktivorous fish (Dolson *et al.*, 2009). Thus, increased predation pressure (actual or perceived) by piscivores on planktivores in reticulate lakes could have promoted pelagic zooplankton diversity via reduced fish planktivory. The link between lake shape and diversity is also consistent with previous observations on fish, protozoa and diatom communities in various river networks (Carrara *et al.*, 2012; Liu *et al.*, 2013; Muneepeerakul *et al.*, 2008), but ours appears to be the first mention for lakes and zooplankton diversity. Moreover, in agro-ecosystems, plant diversity has also been positively linked to habitat geometric shape complexity (Moser *et al.*, 2002), including effects associated to human-induced rectangularity to landscapes. It is also possible that reticulate lakes act more as metacommunities, wherein dispersal limitation between lobes, each promoting its own compositional diversity through specific local conditions (e.g., differences in depth, littoral habitat, fish species, lotic inputs), would promote overall greater ecosystem diversity than in round lakes, where more physical homogenization could potentially reduce overall diversity. However, increased richness in more reticulate lakes did not correspond to major shifts in zooplankton community composition, since lake circularity did not plot strongly in the taxonomic RDA and was not included in the forward-selected variables of the functional RDA (Figure N.1 in Annexe N).

2.5.2 Agriculturally-dominated regions have distinct diversity

The most unexpected diversity response to environmental factors was the positive correlation between *FRic* and the fraction of agriculture in the watershed as observed in the PCA, related also to high nutrient and ion concentrations. Across Canada, agriculture appeared to be the most important variable separating sites with high and low *FRic* (Annexe H); a significant and overall positive relationship also emerging in the GAMMs (Annexe J). However, this positive continental trend was mainly driven by sites from the Arctic Ocean basin and Great Lakes-St. Lawrence, regions of moderate agriculture activities (Annexe J; *FRic*). Meanwhile, in sites from the Hudson Bay basin (which includes the Canadian Prairies ecozone, where most of the extensive agriculture occurs in Canada), *FRic* was negatively related to agriculture as would be expected. Indeed, intensive pesticide use is of growing concern for freshwater ecosystems in agricultural regions with a variety of documented negative effects on zooplankton, including altered sex ratios, modified population dynamics and reduced abundances or diversity (Hanazato, 2001; Hasenbein *et al.*, 2016; Hébert *et al.*, 2021). However, a positive relation between diversity and agriculture-related variables, as we report, has also been previously observed and ascribed to an increase in the relative biomass of small zooplankton species as the more efficient herbivores such as *Daphnia* are lost and energy transfer from phytoplankton to zooplankton is reduced (Hanazato, 1998; Havens et Hanazato, 1993). However, we noted no obvious relationships between community weighted body size means or diversity and agriculture (results not shown). Moreover, in the RDAs, agriculture was not associated with reduced *Daphnia* species biomass, nor with smaller taxa. Instead, we observed that *Daphnia pulicaria,* a species recently demonstrated to have local adaptation favoring high biomass in hypereutrophic lakes (Moody *et al.*, 2021), were more prevalent in lakes with higher fractions of agriculture in the watershed. Since *FEve* and *FDis* (metrics affected by species biomasses) did not respond in the same positive way to agriculture as did *FRic*, we infer that the most impacted sites were dominated by a few generalist species (mainly *Daphnia pulicaria* from the compositional RDA) harboring similar functional traits (related to large body size; Figure N.1). Our results indicate that even in regions of moderate activities, agriculture is a dominant driver of zooplankton structure and diversity, which could have cascading effects on lake food-webs and potentially interact with nutrients to influence the degree of algal blooms.

Agriculturally-dominant regions were also characterized by higher nutrient and ion concentrations that in turn were significant predictors of zooplankton diversity and assemblages. Primary production is often regulated by phosphorus availability in temperate lakes, which in turn affects zooplankton diversity. Zooplankton taxonomic richness has generally been associated to chl*a* or TP concentrations and related to bottom-up processes (Barnett et Beisner, 2007; Dodson *et al.*, 2000). However, a clear diversity-production relationship pattern was not observed in our study as we were expecting. Instead, we noted a significant nation-wide reduction in taxonomic and functional diversity (Shannon, richness, rarefied richness and *FDis*) in relation to hypolimnetic TP concentration, which can reflect maximum potential TP concentrations. However, important differences were observed among continental basins as revealed by the GAMMs. Regional taxonomic diversity showed either unimodal or negative relationships to TP, while *FDis* showed an overall reduction along the TP gradient, dominated by responses from the Pacific and Arctic Ocean basins (Annexe J). A similar pattern between functional (but not taxonomic) diversity and TP was observed previously in 18 lakes in eastern Canada (Great Lakes-St. Lawrence basin; Barnett and Beisner 2007). This pattern was attributed to reduced vertical phytoplankton spatial heterogeneity within lakes with increasing TP, which might also explain our results and would benefit from further research. Our findings are critical in understanding the effects of trophic status on lake ecological function, as reduced crustacean zooplankton diversity in more productive lakes could have important top-down effects or alter predator–prey dynamics. Our results also suggest that diversity-production models should consider regional heterogeneity captured at the continental basin scale.

2.5.3 Zooplankton response to water quality metrics

In contrast to the diversity data, the greatest portion of total variation in zooplankton taxonomic and functional compositional data was explained by water quality over morphometry and land use variables across Canada. The same pattern emerged within all continental basins, except for the Atlantic Ocean basin (where morphometry explained slightly more variation than water quality; Table 2.3). We also observed strong responses of zooplankton diversity to water quality variables. Indeed, we detected significant effects of a range of chemical variables including pH, temperature (and related water pressure), colour, DO, DOC, sodium and nutrients. Similarly, in a study of 54 lakes in Quebec (Canada) Pinel-Alloul *et al*., (1995) demonstrated that abiotic factors, and especially water chemistry variables, were the main drivers of variation in zooplankton communities.

In terms of water quality, calcium declines have been of increasing concern in Canadian Boreal lakes over the past few decades, associated with historical acid deposition and logging in watersheds (Jeziorski *et al.*, 2008; Watmough *et al.*, 2003). Interestingly, calcium was not retained in any of our RF models conducted at a national scale, neither was it selected in the taxonomic compositional RDA. However, our PCA shows strong negative correlation between calcium and taxonomic richness as we expected in our initial hypotheses. Furthermore, in the 314 lakes subset, we observed a lower *FRic* at low Ca concentrations in the Great Lakes–St. Lawrence and

Atlantic Ocean drainages, but weak or opposing patterns in other regions (Annexe K). In the coming years, 37% of lakes in south-central Ontario (Great Lakes-St. Lawrence basin) are expected to experience calcium declines below the threshold of 1.5 mg Ca/L at which growth and reproduction of *Daphnia* is reduced (Reid et Watmough, 2016). The negative effects of declining calcium concentrations observed previously on crustacean zooplankton (including increased mortality combined with reduced growth and reproductive rates; Azan *et al.* 2015; Azan and Arnott 2016) were not detectable at the pan-Canadian scale, where many factors interact to affect diversity. However, we did find evidence of a significant association between zooplankton *FRic* and calcium in certain regions (Great Lakes–St. Lawrence and Atlantic Ocean basin, 314 lakes subset).

Increasing concentrations of chloride associated with road salt application is another issue of growing concern in urbanised watersheds as freshwater salinization negatively affects zooplankton reproduction, mortality and composition (Arnott *et al.*, 2020; Hintz et Relyea, 2019). Here, we report limited effects of chloride concentration and were unable to determine a diversity threshold from the URTs at a national scale. However, chloride was a significant predictor of *FRic* across Canada, with a general trend of increased *FRic* along the chloride gradient, for all continental basins besides Hudson Bay, where we observed a unimodal response of *FRic* to increased chloride (Annexe J). Moreover, this positive trend was observed despite the fact that chloride concentrations exceeded the current 120 mg Cl^-/L water quality guidelines for aquatic life chronic exposure in Canada (CCME, 2011) for 28 lakes, located mostly in the Hudson Bay basin. As we were expecting, sodium concentrations showed strong negative effects on total and rarefied taxonomic richness, again especially in the Hudson Bay basin, with an identified threshold of around 100 mg/L (Annexe J). Such negative effects of salinity on zooplankton were expected and have been documented previously (Gutierrez *et al.*, 2018; Jeppesen *et al.*, 2015). On the other hand, richness in the Pacific and Arctic Ocean basins showed a positive correlation to sodium concentrations. A possible explanation for this positive effect is that the zooplankton communities from the associated ecozones (Boreal Cordillera, Taiga Cordillera and Taiga plains) were dominated by *Leptodiaptomus* species (Paquette *et al.*, 2021), which are considered to be salt-tolerant taxa owing to their marine origin (Sarma *et al.*, 2006). Nation-wide, however, we observed that increased sodium concentrations were more strongly associated with *Daphnia pulicaria,* a species known to be relatively resilient to high salinity (Wersebe *et al.*, 2021) and which dominated in the agricultural region of the Prairies (Hudson Bay basin). We suspect that these regional patterns inhibited the detection of a nationwide negative response pattern in more urban sites where road salt is added in high quantities.

2.5.4 Moderate influence of fish metrics on zooplankton

Top-down regulation by fish predation has been demonstrated to play a major role in structuring zooplankton communities (e.g., Gliwicz, 2003) with changes in the dominant trophic position of fishes in a lake (planktivore or piscivore), having cascading effects on lower trophic levels (Carpenter *et al.*, 2001). In contrast to our expectation, the effect of fish predation variables on zooplankton taxonomic and functional composition was always minimal relative to the effects of all other groups of variables (morphometry, land use and water quality) in our study. Furthermore, no thresholds in fish maximum trophic level or in planktivore or piscivore richness were identified as critical for zooplankton diversity. These results could be an artefact of our lack of fish abundance data, but a previous survey of 52 lakes in Ontario (Canada) also found that fish abundance (CPUE) had no significant effect on zooplankton species composition (Shaw et Kelso, 1992). However, it is also possible that fish predation variables are actually less important relative to those of the environment at a continental scale. Indeed, in our non-linear models where slopes and intercepts were allowed to vary by region, planktivore richness did emerge as a significant predictor of taxonomic and functional richness, with a general pattern of increased zooplankton diversity at higher planktivore richness (Figure 2.5). In a previous study, Hessen *et al*., (2006) also found greater zooplankton richness in lakes dominated by planktivore fish species. The authors hypothesized that elevated zooplanktivory could lead to a release of zooplankton competition, leading to greater richness, aligning with our findings. However, our results indicate that the positive effect of planktivory on zooplankton diversity is modest compared to that of lake morphometry or water quality variables.

2.6 Conclusions

By exploring zooplankton diversity and compositional variation over hundreds of lakes across Canada under a wide range of environmental variables, we demonstrated that environmental drivers are important at the continental scale. We also observed a hierarchy in the importance of environmental variable types, with lake morphometry variables being a major control of zooplankton diversity but water quality metrics being more critical to community compositional variation. Water quality variables including macronutrients, calcium, chloride and sodium did, however, play contrasting roles among continental basins. By incorporating both taxonomic and functional diversity indices we were also able to reveal environment processes and diversity-environment relationships that would have remained undetected using only traditional taxonomic approaches.

Although we were able to explain a fair amount of variation in zooplankton taxonomic and functional diversity for a lake survey with our extended environmental data set, much variation remained unexplained. The main potentially relevant drivers of zooplankton diversity not explored in this study are climate variables, as these have been demonstrated to be important controlling factors for zooplankton diversity (e.g., Patalas 1990; Pinel-Alloul *et al.* 2013). It should also be noted that because of the "snap-shot" sampling design of this study, our results do not represent the important temporal (seasonal) nor spatial variability within lakes. However, the analysis of sediment cores collected as part of LakePulse could eventually help answer important questions about how Canadian lakes have changed over longer scales associated with the Anthropocene. Our conclusions might also be limited by the correlational nature of the study, and multiple analyses performed on the same data. Despite these caveats, our work represents a milestone in improving generalized understanding of anthropogenic impacts on lake zooplankton diversity at the continental scale and highlights the importance of continental watersheds in explaining environmental variability among lakes. Given their central role in lake food webs, shifts in crustacean zooplankton diversity provide an aggregate "sentinel" response of lake biota to climate change and human disturbances, helping to point to particularly important drivers. Our study has revealed that diversity and compositional responses varied by continental watershed, requiring a focus at these spatial scales to identify environmental drivers of change in lake communities.

CHAPITRE 3

ZOOPLANKTON ASSEMBLAGE STRUCTURE AND DIVERSITY SINCE PRE-INDUSTRIAL TIMES IN RELATION TO LAND USE

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Cindy Paquette[1,2,3], Katherine Griffiths[2,3], Irene Gregory-Eaves[2,3] and Beatrix E. Beisner[1,2]

Corresponding author: paquette.cindy@courrier.uqam.ca

[1]Department of Biological Sciences, University of Quebec at Montreal, Montreal, Quebec, Canada;
[2]Interuniversity Research Group in Limnology (Groupe de recherche interuniversitaire en limnologie; GRIL);
[3]Department of Biology, McGill University, Montreal, Quebec, Canada

3.1 Abstract

Aim: While it is now well accepted that human activities are having pronounced effects on natural ecosystems, regional variation in the rate and magnitude of various human impacts is unclear. Moreover, the effects of land use change on natural aquatic communities have only relatively recently begun to be explored. Our goal was to understand how and where assemblages of a central food web component of freshwater lakes have changed over the course of industrialization in relation to land use.

Location: Canada.

Time period: pre-1880 AD to present.

Major taxa studied: Cladoceran zooplankton.

Methods: As part of the Natural Sciences and Engineering Research Council (NSERC) Canadian Lake Pulse Network, we selected 101 lakes across Canada along a gradient of human impact to analyse subfossil cladoceran assemblages from sediment cores. We examined relationships between taxonomic and functional indicators of clad- oceran assemblage change among lakes and through time.

Results: Contemporary assemblages were taxonomically and functionally less diverse locally relative to pre-industrial assemblages (α-diversity) and were structured by the degree of human impact in watersheds. Local α-diversity losses were greatest in highly impacted lakes where agriculture and pasture are prevalent. While spatial homogenization (spatial β-diversity) did not increase since pre-industrial times as expected, temporal turnover (temporal β-diversity) showed a non-significant but increasing trend in highly impacted lakes, especially in urbanized watersheds.

Main conclusions: Cladoceran assemblages have changed significantly over the course of the Industrial period, and especially in more highly impacted watersheds, underscoring the important role of watershed land use in shaping diversity. However, indicators of cladoceran function have remained relatively conserved over time and land use change showed little impact on β-diversity, despite important environmental variation. Overall, this research furthers

our understanding of the health status of Canadian lakes and the consequences of human activities, especially agriculture and urbanization, on lake zooplankton.

3.2 Introduction

Lakes are important sentinels of climate and other anthropogenic changes as they accumulate runoff from whole watersheds, thereby integrating factors from across the catchment, potentially reflecting landscape changes. Because global sources of freshwater are facing unique threats, including land use impacts and climate change, it is becoming increasingly urgent to improve our understanding of how lakes may change in response to various stressors. Determining the long-term ecological impacts of the factors that affect aquatic ecosystems is crucial for understanding current and future lake health. A recent review of the effects of multiple stressors on aquatic eco-systems revealed that most limnological studies considered time periods between 7.5 to 9 years (based on a targeted search from the ISI Web of Science citation databases that yielded 219 papers; Nõges *et al*., 2016). However, in many cases, such relatively short timescales will fail to include baseline conditions prior to the onset of multiple stressors and instead examine what are already changing and transient conditions. While Canada is home to more lakes than any other nation (Messager *et al.*, 2016), long term monitoring of Canadian lakes is rare (Smol, 2019). Although dating sediment records is subject to some error, the analysis of lake cores can fill key knowledge gaps by evaluating changes between current conditions and those present before the onset of industrialization (i.e., at least pre-1880 CE).

In this context, crustacean zooplankton are useful indicators of change because they occupy a central role in lake food webs, mediating bottom-up energy and biomass transfer towards fish, and top-down predation effects extending to the lower food web, including control over phytoplankton dynamics. Cladocerans in particular are powerful palaeolimnological indicators as their exoskeletons preserve in lake sediments for centuries. Certain exoskeleton parts (i.e., carapaces, post-abdomens, claws, mandibles, and head-shields) can be used to identify subfossilized cladoceran species or species complexes (Korhola et Rautio, 2001). Subfossil cladoceran records can thus be used to track the history of changes in lakes and their catchment conditions, thereby providing information on various (and usually long-term) effects including climate change (Zawisza *et al.*, 2017), fish introduction (Berta *et al.*, 2019), trophic changes (Cheng *et al.*, 2020), water quality (Korhola et Rautio, 2001), calcium concentrations (Griffiths *et al.*, 2019; Jeziorski *et al.*, 2008), lake productivity (Hann *et al.*, 1994; Korponai *et al.*, 2011), pH (Labaj *et al.*, 2021), metal contamination (Winegardner *et al.*, 2017), and planktivory pressure (Amsinck *et al.*, 2005b; Davidson *et al.*, 2007). Subfossil cladoceran assemblages may also provide a more integrative, whole-lake portrait than discrete pelagic samples of contemporary communities because the sediments deposited in the deepest part of a lake contain particles focused potentially from the entire lake basin, including the littoral zone (García-Girón *et al.*, 2018; Jeppesen *et al.*, 2011) Likewise, a sediment layer 1 cm in thickness often integrates multiple years of deposition (Baud *et al.*, 2022).

While many ecological studies focus on changes in α-diversity (local scale) alone, compositional turnover (β-diversity) has been demonstrated to be a useful tool in conservation, as it represents a sensitive metric of variation (taxonomic or functional) in communities among sites (spatial) or through time (temporal) (Figure 3.1). Because of climate change, human activities, and the creation of artificial connections between lakes by humans, lake biotic communities are becoming increasingly homogenized at a landscape scale (Lockwood *et al.*, 1997; McGill *et al.*, 2015; Olden *et al.*, 2004). This spatial or temporal homogenization of community composition can be determined using β-diversity (Legendre, 2019; Winegardner *et al.*, 2017). Moreover, the use of functional traits can add additional insights into the ecological consequences of community shifts at large spatial scales. Functional β-diversity, the functional dissimilarity among communities, provides an opportunity to relate temporal or spatial community changes to ecosystem functioning and better determine the impacts of biodiversity losses (Crabot *et al.*, 2020; Simões *et al.*, 2020). The combination of α-and β-diversity, along with taxonomic and functional approaches enables a robust assessment of biodiversity changes and potential impacts on ecosystem functioning.

In this first pan-Canadian study of long-term cladoceran dynamics from the past ~ 150 years, we compared contemporary and pre-industrial sediments to characterize the relatively undisturbed state of lakes and to identify how cladoceran assemblages have changed since preindustralization. Identifying the sites and regions with the greatest shifts in assemblages can help in our assessment of where aquatic ecosystems have been the most affected by climate change or other human activities. This project is part of the NSERC Canadian Lake Pulse Network, the goal of which is to evaluate the health status of freshwater lakes across the country by assessing changes since pre-industrial times to aid in determining how they may continue to change in the future (Huot *et al.*, 2019). Based on an analysis of the spatial patterns in contemporary crustacean zooplankton community composition and diversity across the 624 lakes used in this study, biogeography was shown to best align with continental watersheds delineations (Paquette *et al.*, 2021). Contemporary pelagic communities were also related to > 40 environmental, morphometric, land use and fish variables, revealing an important, present-day heterogeneity across Canadian lakes, with divergent effects of environmental drivers among continental basins (Paquette *et al.*, 2022). Furthermore, in a subset of 33 eastern Canadian lakes, sub-fossil cladoceran assemblages were analyzed together with diatom and chironomid remains in multi-factor analyses to identify key co-responses among trophic groups in response to important environmental variables, including lake morphometry, water quality, and land use parameters (Griffiths *et al.*, 2021). However, this study did not address changes nation-wide in zooplankton assemblages since pre-industrial times.

Previous cross-lake comparisons of zooplankton sub-fossil assemblages have focussed on surface sediments assemblages across hundreds of lakes in Alaska and Canada (e.g., Labaj *et al.,* 2021) and detected the primary importance of lake depth and pH. Furthermore, in contemporary zooplankton community comparisons across lakes, land use gradients have been identified as significant predictors (Albert *et al.*, 2010; Dodson *et al.*, 2005, 2007). To expand on the findings of these studies, we set out to evaluate the relationship between modern land use and zooplankton assemblage shifts since pre-industrial times across Canada for a subset of 101 of the LakePulse lakes.

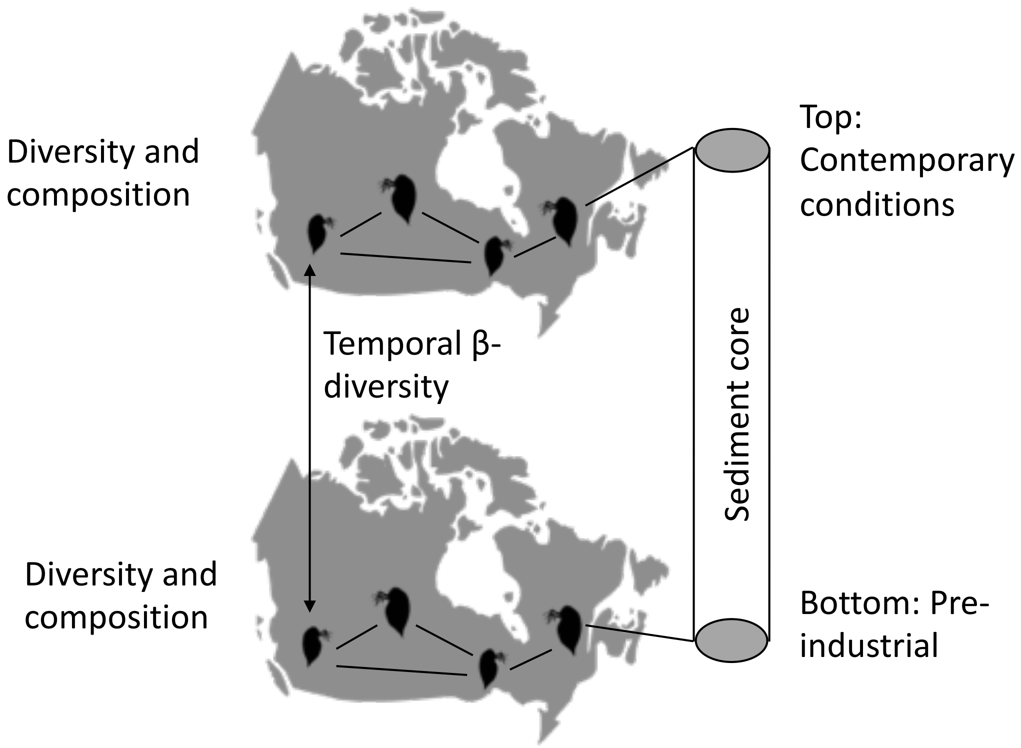


Figure 3.1 Schematic diagram of the sub-fossil cladoceran community comparisons made in this study. Local taxonomic and function diversity and composition were analysed separately among lakes (represented by *Daphnia* symbol) in both the contemporary and the pre-industrial assemblages was also analysed for each lake. Adapted from Winegardner *et al.* (2017).

With the incorporation of taxonomic and functional zooplankton composition as well as investigating the variation in α- or β-diversity, we were able to test new hypotheses, especially with respect to cladoceran functional turnover through time (temporal β-diversity). First, we hypothesized that sites with more intensive human watershed land use would affect cladoceran composition through altering near shore environments and enriching lakes with nutrients and ions. We pre- dicted that (a) contemporary cladoceran taxonomic, and to a lesser extent functional composition would differ among lakes according to the level of human impact in the lake watershed, an index based on watershed land use type (see Methods for details). Second, we hypothesized that the extent of land use would reduce α-diversity patterns through time. We predicted that (b) local (α-) diversity would decline in modern relative to pre-industrial times, with the greatest reductions in currently highly impacted lakes, and especially in watersheds with extensive agricultural activity. We then hypothesized that the degree of spatial homogenization of the assemblages would vary between time points, predicting that (c) differentiation among lakes (spatial β-diversity) would be more prevalent in pre-industrial assemblages than contemporary ones. Finally, we examined associations between temporal turnover and land use, predicting that (d) greater human watershed activity (degree of human impact and type of land use) would increase temporal turnover (temporal β-diversity) of the assemblages since pre-industrial times.

3.3 Methods

3.3.1 Lake selection and sediment sampling

Over the course of three summers (2017-2018-2019), 664 lakes were sampled covering six drainage basins across Canada as part of the NSERC Canadian Lake Pulse Network. Lakes within 1km road access were randomly selected following a stratified design according to ecozone, lake size and human impact class (see Huot *et al.*, 2019). Owing to the large time investment needed for sub- fossil cladoceran identification, a subset of 101 focal lakes was selected (Figure 3.2). The subset of lakes was chosen to maintain the same stratified sampling design as the full survey (i.e., attempting to equally sample across ecozone, lake size, and human impact class) while selecting sites with cores long enough to reach pre-industrial conditions (i.e., cores that exceeded the target core length, see details below, such that the bottom samples were likely at least pre- 1880 in age).

In each lake, sediment cores were taken from either the deepest point of the lake or a deep basin (located with bathymetric maps or depth finders) using a gravity corer (Blomqvist, 1991). Cores were sectioned on-site and samples were collected using a vertical extruder. Sediment samples were stored in 60-ml Fisher, pre-weighed sterile specimen cups in the freezer. The targeted sediment core depth varied among ecozones, with the ecozones hosting more productive lakes such as the Prairies, Boreal Plains, and Semi-Arid Plateaux requiring longer cores (at least 47 cm), while the remaining ecozones had a target length of at least 32 cm. The ecozone-specific target core lengths were calculated using sedimentation rate estimates based on published records for each ecozone (summarized in Griffiths *et al.*, 2021; Alexandre Baud pers. comm.) with the goal of reaching pre-industrial conditions (i.e., at least pre-1880).

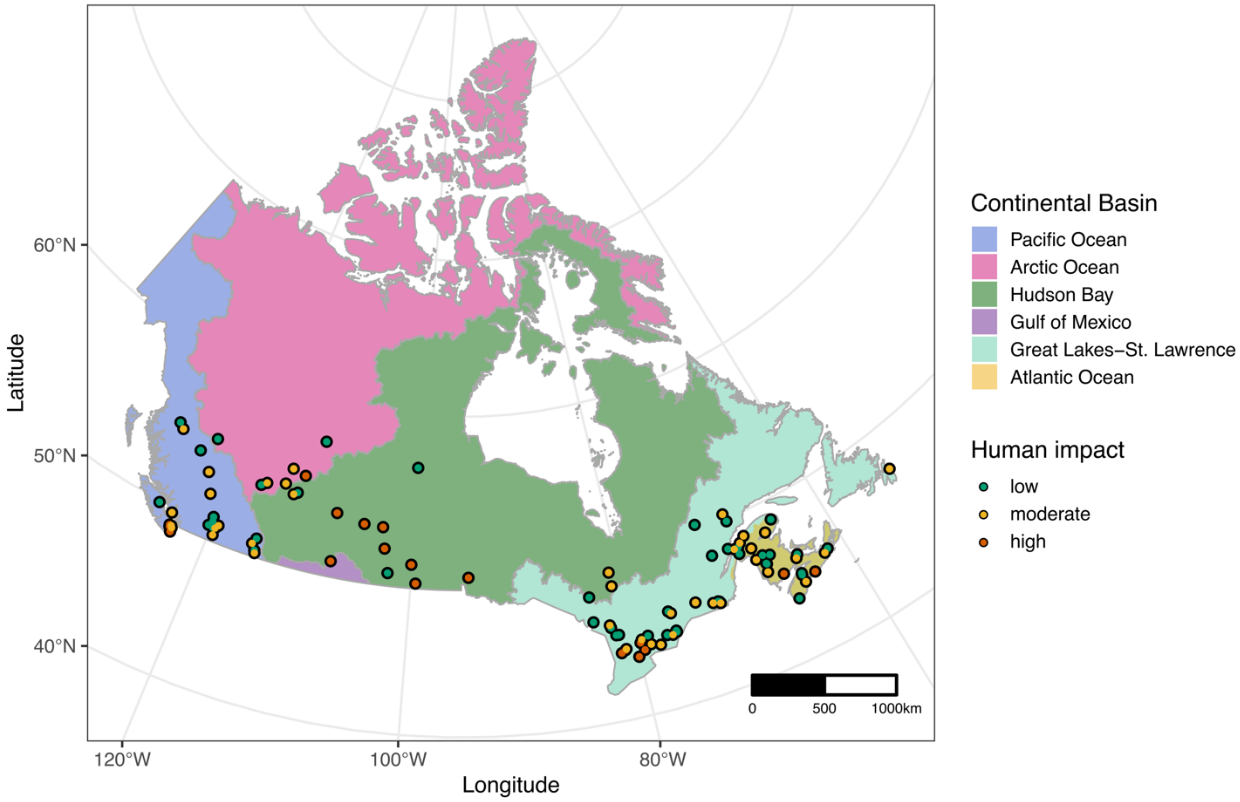


Figure 3.2 A map showing the position of the 101 lakes sampled by the NSERC Canadian Lake Pulse Network for sub-fossil cladocera. Lakes are contoured by the differently colored continental basins and colored by human impact class (human impact index <0.1 is low ; moderate 0.1-0.5 high >0.5). Map created using Canada Atlas Lambert projection (NAD83 CSRS).

A 'top– bottom' or 'before and after industrialization' approach was used in this study, where the top sample was the first centimetre of the surface of the sediment core, representing contemporary lake conditions. The bottom sample corresponded to the 1 cm of sediment located between 3 and 4 cm from the base of the core [(x – 4)–(x – 3), where x is the length of the core], representing historical conditions, before industrialization. In a subset of 87 cores, ^{210}Pb and ^{214}Bi activities in the bottom samples were measured using gamma spectrometry following the methods outlined by Schelske *et al.* (1994) and the activities of the two isotopes were compared to ensure that the bottom sample represented pre-industrial conditions (at least pre-1880). Background conditions were assumed to have been reached when ^{210}Pb activity was no different or lower than ^{214}Bi activity in the bottom sediment sample (within error bars representing one standard deviation; see Figure P1 in Annexe P). Additionally, full cores were collected in a subset of 27 lakes (Figure P2 in Annexe P) to analyse ^{210}Pb activity profiles with a gamma well detector. These profiles were used to estimate sediment mass accumulation rates and potential changes in temporal resolution between top and bottom samples (Baud et al. 2022). Further details on sediment dating and sedimentation rate estimations are provided in Griffiths et al. (2021) and Baud et al. (2022).

3.3.2 Cladoceran preparation and identification

Cladoceran extraction and preparation generally followed the protocol from Korhola and Rautio (2001). Briefly, ~ 0.2 g of freeze-dried sediments were digested with 10% of potassium hydroxide (KOH) solution, heated for 30 min, and rinsed with deionized water onto a 36 µm sieve. Extracted cladoceran samples where then preserved in vials with a few drops of ethanol and colored with 3-5 drops of glycerin-safranin solution. Slides were mounted using 1 to 5 aliquots of 80 µL digested sediments and glycerine jelly solution. All sub-fossil cladocerans were identified by a single taxonomist across all sites, using DM 2500 Leica compound inverted microscope under 200X-400X magnification. Identification at the species or genus level was done using the taxonomic keys Szeroczynska and Sarmaja-Korjonen (2007) and Korosi and Smol (2012b, 2012a). *Bosmina coregoni* was differentiated from *Bosmina longispina* based on the chitinous thickening around the headpore. Entire coverslips were scanned, until minimal count of 100 total individuals was reached. Individual numbers were calculated by enumerating the most abundant fragment of each taxon (Kurek *et al.*, 2010; Zharov *et al.*, 2021).

Taxa were classified functionally using species-trait information from DeMott and Kerfoot (1982); Barnett *et al.* (2007); Griffiths *et al.* (2019) and Paquette *et al.* (2021). The functional traits used were: resource acquisition (B(*Bosmina*)-filtration, C(*Chydorus*)-filtration, D(*Daphnia*)-filtration, S(*Sida*)-filtration, or raptorial), habitat (littoral, pelagic or intermediate), trophic group (carnivore or herbivore), and species mean size.

3.3.3 Human impact classification

Lakes were classified into three human impact classes (low, moderate or high) based on a quantitative human impact index calculated from the fractions of land use types in the watershed of each lake. The fractions of land use types (urban, mines, agriculture, pasture, forestry and managed grassland), and the fractions of water versus natural landscape in the watershed of each lake were provided by the Lake Pulse Network as described in Huot *et al.* (2019). The Lake Pulse Network watersheds were delineated using flow direction, which was calculated with the Canadian Digital Elevation Model (Government of Canada, 2015). Values of 0 (water, natural landscape), 0.3 (managed grassland) 0.5 (pasture, forest loss) or 1 (urban, mines, agriculture) were then applied to the different types of land use. The human impact index, varying between 0 and 1, represented the mean of all the values across each cell in the raster layer of land use within a watershed (See Huot et al. 2019 and Table Q1 in Annexe Q for details). Lakes with a human impact index < 0.1 were then arbitrarily attributed a class of "low" (n=43) impact; lakes ≥ 0.1 and < 0.5 had a "moderate" impact (n=39), and lakes with an index ≥ 0.5 were classified as "high" impacted lakes (n=19).

3.3.4 Statistical analyses

All statistical analyses were performed using R v. 4.1.0 (R Core Team, 2021).

3.3.4.1 Compositional distinctness among human impact classes

Canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) was used separately on top and bottom assemblages to assess the distinctness of cladoceran taxa or functional traits to the different human impact classes. Square root transformed relative abundances of dominant taxa (i.e., those taxa with greater than 2% abundance in at least 1 sample; the equivalent of Hellinger-transformed abundances) were used with the *CAPdiscrim()* function of the 'BiodiversityR' package (Kindt, 2020). The "Bray" distance was used to calculate the country-wide percentage of correct predictions, as well as the percentage of correct attribution of the lakes to each land use classes using the taxonomic or the functional compositions. Multivariate analysis of variance (MANOVA) was used to assess the significance of the model, predicting differences in composition among land use classes compared to that of randomized data. In the functional CAP, species were classed as either “small” or “large” taxa, using a species size cut-off of 0.5 mm, to retain only categorical traits. Then the frequency of each functional trait classes (i.e., functional composition) was computed with the functcomp() function of ‘FD’ R package (Laliberté *et al.*, 2014).

3.3.4.2 α-diversity estimation

The relative abundances of taxa in either the top or bottom samples were used to compute taxonomic and functional diversity indices (Figure 3.1). Taxonomic species richness, Shannon entropy, Simpson diversity and Pielou's evenness were computed using *diversity()* in ‘vegan’ package (Oksanen *et al.*, 2019). Rarefied richness was rounded to 93 individuals (unidentified individuals were removed from the analysis, reducing the minimum count size) in the top samples, and 100 individuals in the bottom samples. Functional evenness (FEve; Villéger *et al.*, 2008), functional dispersion (FDis; Laliberté et Legendre, 2010) and functional richness (FRic; Villéger *et al.*, 2008) were estimated with the *dbFD()* function and Gower distances in the ‘FD’ package (Laliberté *et al.*, 2014). The percentage of change between the pre-industrial and the contemporary cladoceran assemblages was calculated for each taxonomic and functional diversity index according to the human impact class [i.e., for each human impact class: (diversity Bottom - diversity Top)/diversity Bottom*100]. Student t-tests were computed between top and bottom values for each human impact class to assess the significance of change. It should be noted that no significant relationships were found between diversity indices and estimated sediment mass accumulation rates in the 27-core subset where these data were available, indicating that diversity patterns were not likely influenced by differences in the temporal resolutions represented by the sediment slice among and within cores (i.e., between top and bottom samples; Figure P2 and P3a in Annexe P).

3.3.4.3 β-diversity estimation

Taxonomic homogenization through time was analysed using Temporal β-diversity Indices (TBI, Figure 3.1; Legendre, 2019), using the *TBI()* R function, 9999 permutations and the Hellinger dissimilarity coefficient (square root followed by chord transformation) for the two time points of each lake. This function provides a vector of TBI between observations from the top and the bottom assemblage of each lake, as well as *p*-values identifying exceptional lakes based on compositional differences computed by permutation tests (and associated *p*-values corrected for multiple testing with Holm's procedure). Mean TBI values were compared among human impact classes using Analysis of variance (ANOVA). *TBI()* was also run using the Jaccard dissimilarity to compute the number of lakes experiencing temporal losses or gains of taxa, which is not possible using the Hellinger dissimilarity. The difference between species gains and losses was tested by parametric and permutational paired t-tests within the TBI function. Temporal taxonomic β-diversity was also compared to mass accumulation rate differences between the top and bottom samples, revealing no effect of sedimentation rates on temporal cladoceran homogenization (Figure P3b in Annexe P).

Functional temporal β-diversity was estimated based on the method developed by Legendre (2019). First, joint functional composition for the top and bottom sites was obtained with *functcomp()*, using only categorical traits as in the functional CAP. Gower dissimilarities were then computed from the functional composition matrix, using equal weights for each trait. Principal coordinate analysis (PCoA) was then applied to the square-root transformed Gower dissimilarity matrix. The principal coordinate matrix was then separated into top and bottom time points, and all PCoA axes were used in the *TBI()* function with Euclidian distances and 9999 permutations. To compute trait gains and losses between time points, the *TBI()* function was also used directly with functional trait composition data and Jaccard dissimilarity between top and bottom assemblages.

Taxonomic and functional spatial β-diversity was also estimated for both time points, and by human impact class using the same set of analytical methods as in Paquette et al. (2021). Summarily, taxonomic spatial β-diversity was computed on species presence-absence using *beta.div()* function with Jaccard dissimilarity in the 'adespatial' package (Legendre, 2014; Legendre et De Cáceres, 2013). Functional β-diversity was estimated using *multidimFbetaD()* function (Villéger *et al.*, 2008, 2013) with species presence-absence and species coordinates along the first two dimensions of the functional space.

Statistical relationships between taxon or functional trait assemblages by time point (multi-level pattern analysis) were analyzed with the *multipatt()* function from the 'Indicspecies' R package (De Cáceres *et al.*, 2020) with 999 permutations. This indicator value function (IndVal; Dufrêne et Legendre, 1997) returns lists of those species or traits with significant association to contemporary ("winner" species) or pre-industrial ("loser" species) assemblages.

3.3.4.4 Relating diversity and land use types

Relationships among taxonomic or functional diversity indices and land use types were visualized with correlation-based principal component analysis (PCA). The PCA was computed on scaled land use variables using the 'vegan' package (Oksanen *et al.*, 2019), and diversity indices were added passively using *predict()*.

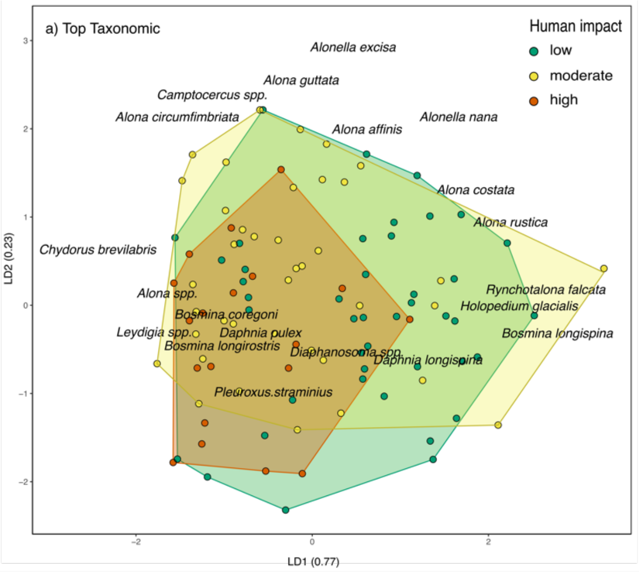
Univariate regression trees (URTs) were used to associate the degree of taxonomic and functional temporal homogenization with land use types and to find thresholds in land use fractions for greater temporal turnover. URTs were computed with the R package 'mvpart' (Therneau et Atkinson, 2014), using 10 cross-validation groups and 100 iterations. The raw fractions of land use in the watershed were used as explanatory variables and TBI as the response variable. The four-group solution tree was selected for taxonomic TBI, and while not being the most parsimonious predictive tree (which had only two groups), it was still within one standard error of the minimal CVRE solution, while not producing too many small groups (Borcard *et al.*, 2018). For functional TBI, the tree with the lowest cross-validation error was selected.

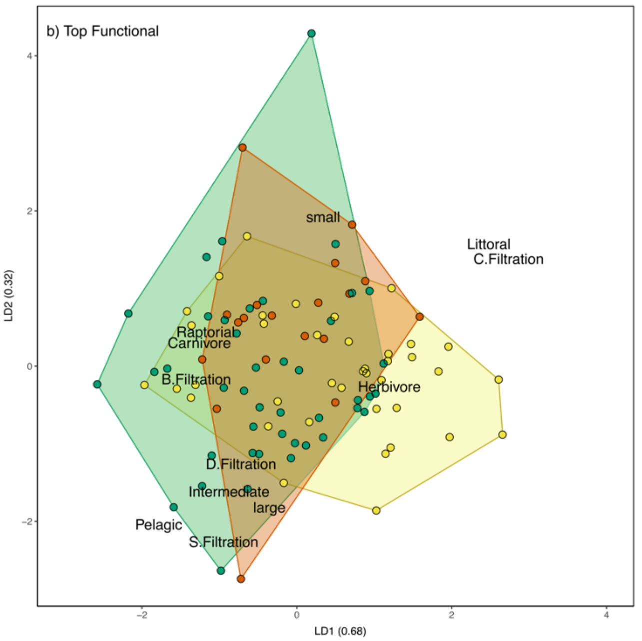
3.4 Results

3.4.1 Taxonomic and functional composition results

Canonical analyses of principal coordinates (CAP) were used to reveal spatial patterns in cladoceran taxa, or functional traits, and human impact classes (Figure 3.3a, Table 3.1). From all four models (taxonomic and functional; top and bottom), only the taxonomic CAP from the top assemblages was significant (*p*=0.01; Table 3.1), indicating a distinctness of contemporary cladoceran taxa among human impact classes. Of the 101 lakes, 55% were attributed to the correct human impact class based on taxonomic composition. Littoral taxa *Chydorus brevilabris* and *Leydigia* spp., as well as the pelagic *Bosmina coregoni* and *Bosmina longirostris* were associated with the high human impact class. Among the taxa associated with low human impact were the littoral species *Rynchotalona falcata* and *Alona rustica*, as well as the pelagic taxa *Bosmia longispina* and *Holopedium glacialis* (Figure 3.3a). The largest difference between top and bottom assemblages was observed in the high human impact class, where the percentage of correct attribution was much greater in the tops (16%, Table 3.1) than in the bottoms (0%). These results suggest that some taxa were significant indicators of the highly impacted lakes under contemporary conditions, while no taxa were associated with these current-day lake attributions under past conditions. Although not significant, the functional CAP from top sediments was able to attribute 50% of the lakes to the correct human impact class. C-Filtration and Littoral functional groups were found to be associated with higher human impact; a trend mainly driven by the response of C. *brevilabris* (Figure 3.3b). It should be noted that the pre-industrial CAP on functional composition could not be plotted since only one axis was significant.

Comparing assemblages between time points with multi-level pattern analysis identified significant indicators as a function of sam- ple interval. Diaphanosoma spp. and B. coregoni were identified with the top samples (‘winner’ species), while Pleuroxus denticulatus was associated with the bottom samples (‘loser’ species). No functional traits were significant indicators of the contemporary or the pre- industrial assemblages.


a) Top Taxonomic
Human impact
low
moderate
high
Alonella excisa
Alona guttata
Camptocercus spp.
Alona circumfimbriata
Alona affinis
Alonella nana
Alona costata
Alona rustica
Chydorus brevilabris
Alona spp.
Rynchotalona falcata
Holopedium glacialis
Bosmina coregoni
Leydigia spp.
Daphnia pulex
Bosmina longispina
Bosmina longirostris
Diaphanosoma spp.
Daphnia longispina
Pleuroxus.straminius
3
2
1
0
−1
−2
−2
0
2
LD1 (0.77)
LD2 (0.23)


b) Top Functional
small
Littoral
C.Filtration
Raptorial
Carnivore
B.Filtration
Herbivore
D.Filtration
Intermediate
large
Pelagic
S.Filtration
4
2
0
−2
−2
0
2
4
LD1 (0.68)
LD2 (0.32)

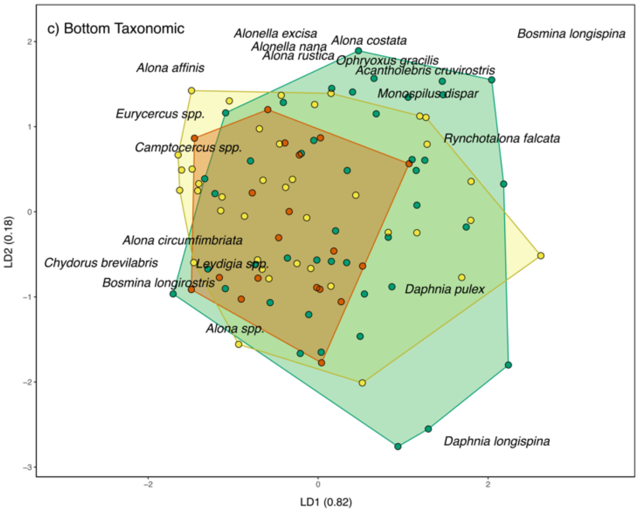

c) Bottom Taxonomic
Alonella excisa
Alonella nana
Alona rustica
Alona costata
Bosmina longispina
Ophryoxus gracilis
Acantholebris cruvirostris
Alona affinis
Monospilus dispar
Eurycercus spp.
Rynchotalona falcata
Camptocercus spp.
Alona circumfimbriata
Chydorus brevilabris
Leydigia spp.
Bosmina longirostris
Daphnia pulex
Alona spp.
Daphnia longispina
2
1
0
−1
−2
−3
−2
0
2
LD1 (0.82)
LD2 (0.18)

Figure 3.3 Canonical Analysis of Principal Coordinates based on Discriminant Analysis (CAP, Scaling = 1) assessing the distinctness of cladoceran (a) contemporary (top) taxonomic, (b) top functional and (c) pre-industrial (bottom) taxonomic assemblages colored by human impact class. The proportion of the between-group variance explained is displayed by each of the linear discriminant axes. Convex hull volumes enclose sites from each human impact class. Only the top 6 taxa strongly associated with LD1 or LD2 were retained to aid visualization. The CAP on pre-industrial (bottom) functional composition was not plotted as only one axis was significant.

Table 3.1 Taxonomic (a) and functional (b) CAP analysis percentages of correct allocation with p-values for the contemporary (Top) and pre-industrial (Bottom) sediments. Across all lakes and for each human impact class, the largest values are highlighted in bold.

(a) Taxonomic CAP by human impact	**Top % correct attribution**	**Bottom % correct attribution**
All	**55.45**	49.50
Low	**69.79**	62.79
Moderate	58.97	58.97
High	**15.79**	0.00
p-value	0.01	NS

(b) Functional CAP by human impact	**Top % correct attribution**	**Bottom % correct attribution**
All	**49.50**	48.50
Low	60.46	**69.77**
Moderate	**61.54**	48.72
High	0.00	0.00
p-value	NS	NS

3.4.2 Temporal patterns in α-diversity

Changes in taxonomic and functional α-diversity indices between pre-industrial and contemporary cladoceran assemblages were compared across Canada and as divided by human impact class. Country-wide, all diversity indices, besides *FRic,* were consistently higher in the past than currently (Table 3.2). When comparing pre-industrial and contemporary nation-wide values, diversity loss was significant for Shannon diversity, total richness, rarefied richness, and *FEve*. Across all lakes, the total richness (gamma diversity) declined from 53 taxa in the pre-industrial assemblages to 51 taxa in the contemporary assemblages. Across all lakes, three species were lost, and one entirely new species was gained, but the latter occurred in only one lake. Species were lost from the assemblages of 57 lakes, while 37 lakes gained species, and seven lakes showed no change in taxonomic richness over time. Paired t-tests showed a significant difference between temporal species losses and gains.

Many lakes experiencing species losses over time were located in central Canada, a region with extensive agricultural activities (Figure R.1a in annexe R). In terms of trait shifts over time, 24 lakes experienced trait losses and 37 lakes gained new traits, while the majority (40) of the lakes showed no change in trait richness. However, the losses and gains in traits over time were not significant and no spatial patterns were noted (Figure R.1b in Annexe R). Among human impact classes, diversity losses between the time-points (top vs. bottom) were always greatest in highly impacted lakes for all diversity indices, with the exception of *FDis* (with non-significant trends for *FRic* and *FEve*; Figure 3.4).

Table 3.2 Total mean taxonomic (a) and functional (b) diversity across all 101 lakes by human impact class. Pre-industrial bottom (left value in each pair) and contemporary top (right value) values are separated by arrows showing the advancement of time. Significant changes from paired t-test between top-bottom pairs are marked by an asterisk with the larger value in bold.

a) Human impact	**Shannon diversity**	**Evenness**	**Simpson diversity**	**Total richness**	**Rarefied richness**
All	**1.51 ->** 1.39 *	**0.56 ->** 0.53	**0.61 ->** 0.58	**15.14 ->** 13.74 *	**13.21 ->** 11.50 *
Low	**1.40** -> 1.35	0.52 **->** 0.52	**0.57 ->** 0.55	**14.86 ->** 13.98	**13.02 ->** 11.73*
Moderate	**1.57** -> 1.51	0.57 **->** 0.57	0.63 **->** 0.63	**15.54 ->** 14.46	**13.49 ->** 12.13
High	**1.65** -> 1.23*	**0.62 ->** 0.50*	**0.67 ->** 0.54*	**14.95 ->** 11.74*	**13.07 ->** 9.68*

b) Human impact	**Functional evenness**	**Functional dispersion**	**Functional richness**
All	**0.67 ->** 0.64 *	**0.19 ->** 0.18	0.31 **-> 0.33**
Low	**0.68 ->** 0.66	**0.18 ->** 0.16	0.34 **->** 0.34
Moderate	**0.68 ->** 0.64*	0.19 **-> 0.20**	0.30 **-> 0.33**
High	**0.64 ->** 0.59	**0.20 ->** 0.18	**0.30 ->** 0.27

3.4.3 Spatial and temporal β-diversity

Spatial and temporal β-diversities were computed across Canada and among human impact classes, revealing overall larger effects of land use on temporal than spatial homogenization. The country-wide taxonomic and functional spatial β-diversities were similar between time points (historical = 0.33, for both taxonomic and functional datasets and modern = 0.35, both taxonomic and functional) and among human impact classes (Annexe S).

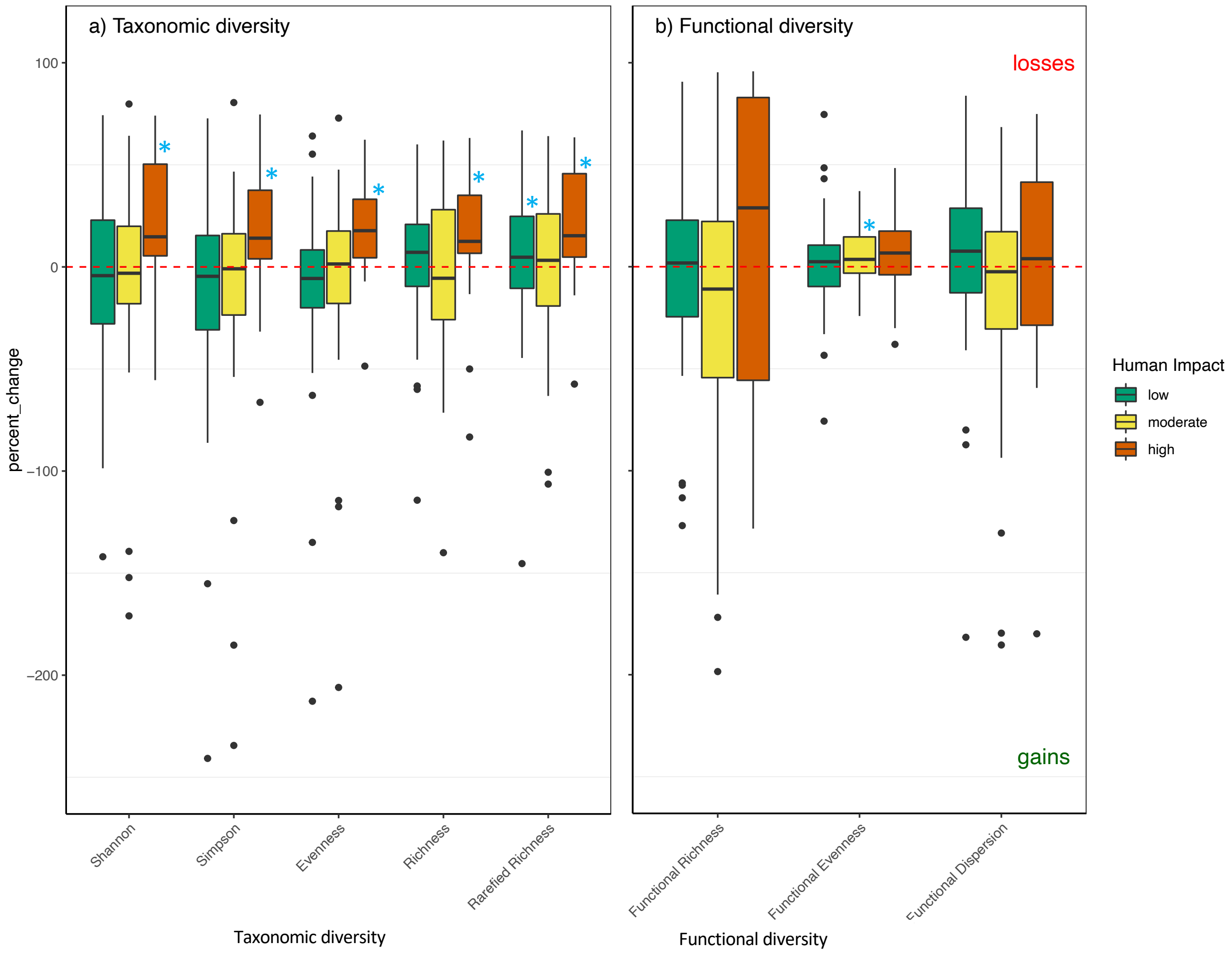


Figure 3.4 Mean (± SE) percent change in taxonomic (a) and functional (b) diversity between the pre-industrial (bottom) and the contemporary (top) cladoceran assemblages across human impact classes. The red dashed line indicates no change, above are diversity losses, and below are diversity gains. Significant changes assessed with paired t-tests between top-bottom pairs are indicated with blue asterisks.

Across all lakes, the metrics quantifying changes in taxonomic or functional β-diversity over time (TBI) had mean values of 0.65 and 0.34, respectively. The temporal taxonomic and functional turnover tended to increase (although non-significantly) under higher human impact class (Annexe R). In particular, five lakes experienced exceptionally large temporal changes in species composition, while nine lakes experienced exceptional temporal shifts in functional composition (*p*-value $\leq$ 0.05 without correction for multiple comparison, Figure S.2 a,b in Annexe

S). There was an overlap of two lakes in Western Canada that showed both extreme taxonomic and functional shifts.

3.4.4 Land use types and cladoceran diversity

A correlation-based principal component analysis (PCA) was used to examine patterns in cladoceran taxonomic and functional diversity with land use. PC1 and PC2 explained 29% and 17% of variance in the land use data, respectively (Figure 3.5). PC1 tracked a gradient of human impact, where lakes of low human land use intensity plotted negatively and were associated with more natural watershed fractions, whilst lakes with intense land uses were mostly associated with high agriculture or pasture in the watersheds. The fraction of water and of urban land use had strong positive loadings on PC2. Passively plotted taxonomic diversity indices from pre-industrial sediments mostly plotted along PC1 and were highest in lakes that are currently dominated by agriculture and pasture. Taxonomic diversity indices from the top sediments were higher in low impact lakes with large fraction of natural landscapes or habitats with forest losses in the watershed. Taxonomic TBI was greater in lakes with high urban land use (Figure 3.5a). Functional diversity indices, both from the contemporary and pre-industrial assemblages, plotted along with a greater range of human impact, but were mostly opposed or were perpendicular to the urban gradient. Functional TBI was higher in sites with lower fractions of natural landscape (Figure 3.5b).

Univariate regression trees (URTs) were used to reveal land use thresholds associated with temporal taxonomic and functional turnover in species composition (Figure 3.6). For taxonomic temporal β-diversity, the fraction of urban land use determined the first split among lakes at a threshold of 4% of urban activities in the watershed. The 66 lakes associated with reduced urban activities were then split by the fraction of forest-loss in the watershed, with a threshold of 2%, while the 35 lakes associated with higher urban activities were differentiated by pasture, also at a threshold of 2%. Lakes with greatest turnover were found in watersheds with ≥ 4% of urban activities and < 2% of pasture (Figure 3.6a). The full tree explained 24% of variance in the temporal β-diversity values. A larger number of land use variables were selected in the functional TBI tree, with urban activities creating the first split at a threshold of 12%. The full tree explained 34% of variance in the functional TBI. Greater mean functional TBI values were observed in lakes with ≥ 12 % of urban activities and ≥ 62% natural landscape (Figure 3.6b).

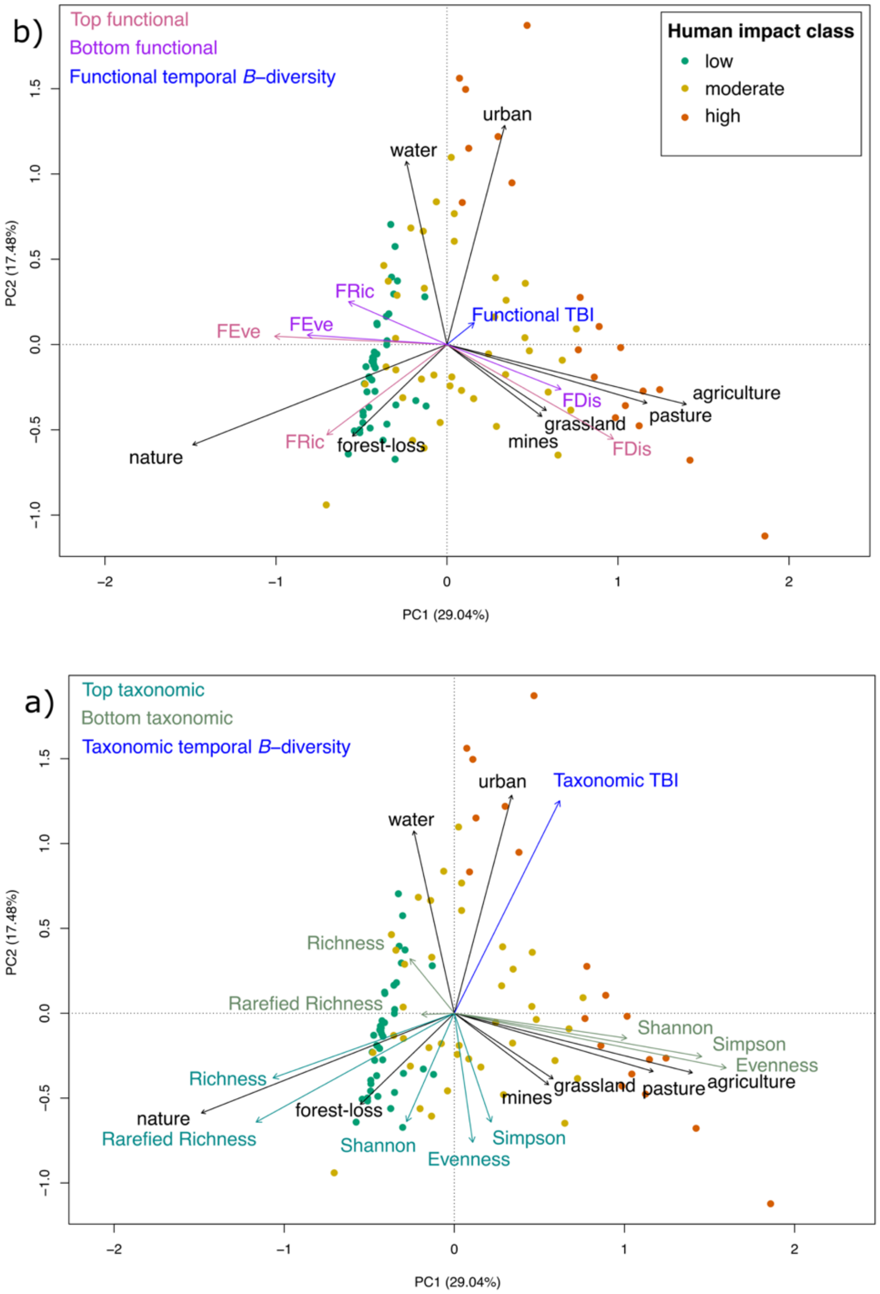
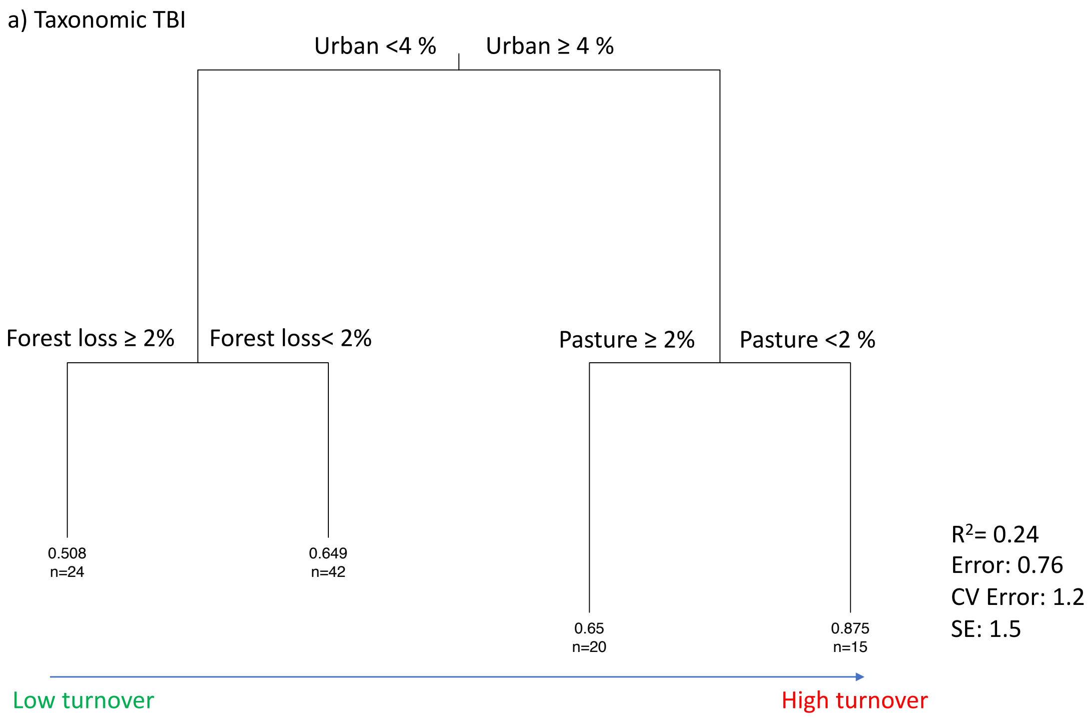


Figure 3.5 Principal component analysis (PCA) on land use variables (scaling 2) for the 101 sites (circles), colored by human impact class, as in Figure 1. Taxonomic (a) and functional (b) diversity indices were added passively. The percent of the site variance explained is displayed by each of the PCA axes.


a) Taxonomic TBI

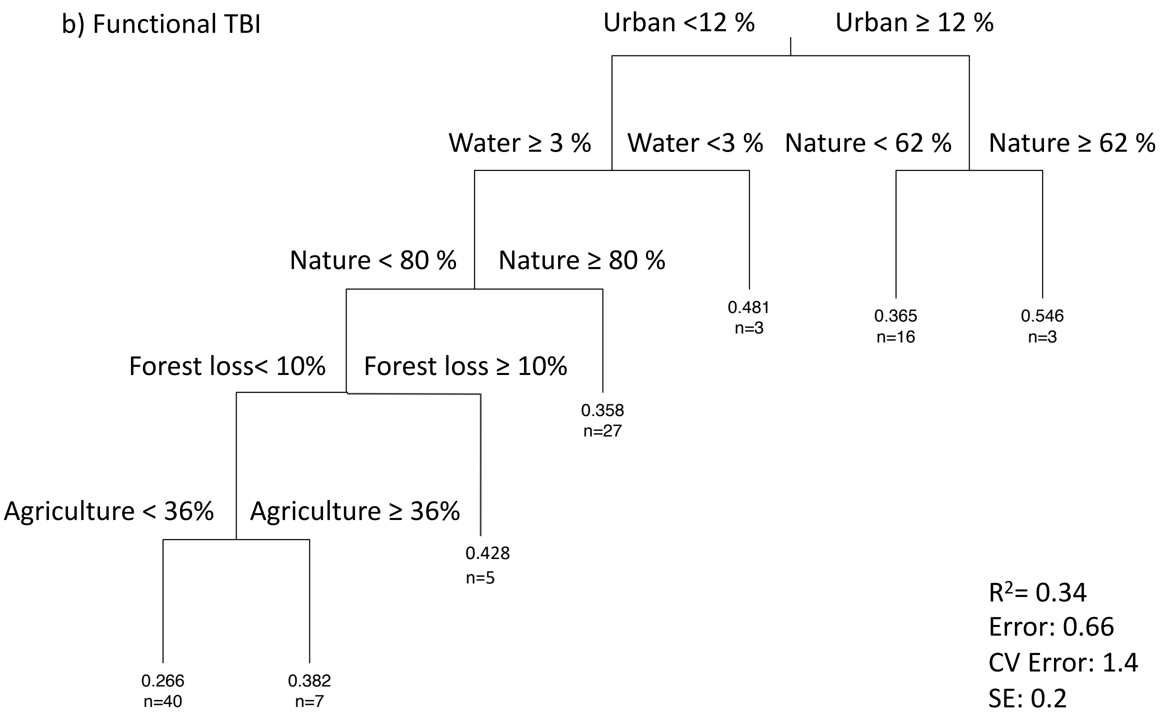

b) Functional TBI

Figure 3.6 Univariate regression tree of the taxonomic (a) and functional (b) temporal β-diversity (n=101) explained by the selected land use variables. The R^2, error, cross-validated error (CV error) and standard error (SE) are provided.

3.5 Discussion

Our analyses of sub-fossil cladoceran assemblages in 101 lakes across Canada offers new insights on the impacts of human activities on aquatic ecosystems over the Industrial period. This study provides the first standardized pan-Canadian analysis of sub-fossil cladocerans, considering temporal changes in composition as well as α- and β-diversity examining both taxonomic and functional dimensions of biodiversity. As expected, the contemporary cladoceran assemblages were structured by human activity levels, especially in highly impacted lakes. We also observed a general reduction in taxonomic and functional α-diversity since pre-industrial times. In highly impacted lakes, more species and traits were lost, and this translated into a modest but non-significant trend of increased temporal turnover along this impact gradient. However, we observed no net loss in species richness country-wide, and no effect of the time-period on spatial β-diversity. Our results demonstrate that cladoceran assemblages and diversity has changed considerably over the course of the Industrial period, especially in highly impacted watersheds, but that the overall functionality of this group has remained relatively resilient over time at the landscape scale.

3.5.1 Contemporary taxonomic, but not functional, composition is structured by human impact

Our first goal was to determine whether cladoceran composition was structured by the degree of human impact, a reflection of the watershed land use. We observed a significant difference in the cladoceran taxonomic composition across human impact classes, but only in contemporary sediments, providing support for our first hypothesis. The main differences observed between past and contemporary composition occurred in the high human impact class, with the identification of specific taxa that were indicators of the current, more intense land use in lake watersheds, which was not the case for these same sites in the past, prior to intense human impact (15.8% of the sites were placed in the correct human impact class based on the cladoceran assemblages in top sediments vs. 0% in bottom Figure 3.3, Table 3.1). Unsurprisingly, *Chydorus brevilabris*, known to be a eutrophic- and salt-tolerant species (Bos et Cumming, 2003; Deasley *et al.*, 2012), was associated with more impacted lakes. The non-indigenous *Bosmina coregoni,* a

Eurasian species first established in the Great Lakes in the late 1960's and currently invading freshwater lakes across Canada (Beaver *et al.*, 2018; Smits *et al.*, 2013; Wells, 1970) was also more prevalent in highly impacted sites (Figure 3.3a) and was significantly associated with top samples (multi-level pattern analysis).

On the other hand, we did not observe any significant association between human impact classes and functional trait distinctness, suggesting that human activities mainly affected cladoceran taxonomic composition in highly impacted sites, but that overall community function in these impacted ecosystems remained relatively stable over time. This result was not unexpected given the high species redundancy in zooplankton functional traits (Barnett *et al.*, 2007), especially when considering solely cladoceran taxa, where many species occupy similar ecological niches. A similar pattern emerged in long-term trends of marine benthic invertebrates, where functional redundancy ensured the resilience of ecosystem functioning despite taxonomic compositional change in the presence of important environmental stressors (Shojaei *et al.*, 2021).

3.5.2 General reduction in taxonomic and functional α-diversity

When comparing the past and contemporary α-diversity, we noted a significant nation-wide reduction in both taxonomic and functional diversity (Shannon, richness, rarefied richness and FEve) over time. However, in examining nation-wide results by human impact class, for all taxonomic diversity indices besides rarefied richness, temporal diversity losses were only significant in the highly impacted lakes (Table 3.2), supporting predictions of our second hypothesis. Our result is consistent with previous findings that human activities are increasing, placing extirpation risks on taxa around the world (Davies et al. 2006). On the other hand, our result is not consistent with global meta-analyses which have recorded no average change in local biodiversity over time (Dornelas *et al.*, 2014, Vellend *et al.*, 2013). Our negative relationship between land use and zooplankton diversity could be related to many factors including eutrophication (Smith et Schindler, 2009), increasing concentrations of chloride associated with road salt (Dugan *et al.*, 2017), or pollutants entering water resources via intensive agriculture (Ribaudo et Johansson, 2007). These factors might also interact with changes in fish predation and introduced species (Li *et al.*, 2022; Sweetman et Finney, 2003) or climate change (Vadadi-

Fülöp *et al.*, 2012) in influencing zooplankton diversity, especially in high impacted lakes. Across Canada, the watershed fraction of agriculture or pasture were the most important land-use categories for taxonomic diversity losses, as observed in the PCA. Indeed, lakes that were historically more species-diverse (bottom samples) were associated with sites that are currently the most impacted by intense land use activities, whereas modern high diversity sites (top samples) are now associated with low human impact scores today (PCA; Figure 3.5a). However, this pattern seemingly did not translate into many significant functional diversity changes (Figure 3.4), and lakes of greater functional diversity showed less movement in the PCA through time in relation to land use (Figure 3.5b). It should be noted that recent increases in global sedimentation rates along with sediment compaction can influence mass accumulation rates of lake sediments (Baud *et al.*, 2021, 2022), and so our temporal local diversity declines could be partially related to more years being integrated in the bottom vs top samples. In our analysis from a subset of 27 dated full cores, we found that the top 1 cm represented on average 11 ± 9 years of deposition, whereas an average of 18 ± 11 years were integrated in the bottom 1 cm interval (for the full cores the bottom was the lowest 1 cm sample that could be dated using ^{210}Pb activities). We also detected a significant increase in sedimentation rates through time [paired t-test p=0.02 between bottom (mean MAR = 0.01 g/cm^2/year) and top (mean MAR = 0.11 g/cm^2/year) samples], yet we observed no relationship between sediment mass accumulation and cladoceran richness (Annexe P). Therefore, changes in sedimentation rate are unlikely the principal factor driving the patterns observed.

Interestingly, a positive correlation between functional richness *(FRic*) and the fraction of agriculture in the watershed, previously observed for entire contemporary crustacean zooplankton communities across 624 Canadian lakes (Paquette et al., 2022) did not emerge in these analyses of the 101 reduced (cladoceran) data set. This lack of correspondance between studies could be related to differences in taxonomic resolution, given that the positive correlation between *FRic* and agriculture across all 624 lakes was related to *Daphnia pulicaria* responses, a taxon that could not be identified to species level in this current subfossil study. Instead, we observed lower *FRic* values in highly impacted sites (Figure. 3.5b), as would be expected given documented negative effects of intensive pesticide use on zooplankton diversity (Hébert *et al.*, 2021; Relyea et Hoverman, 2008). Moreover, in contrast to all other α-diversity indices, *FRic* did not decrease between time points (Table 3.2). The stable functional space of the cladoceran assemblage over time might have been crucial for preventing non-indigenous species from entering the ecosystem when niche space is freed, such as when a species is locally extirpated due to an anthropogenic stressor (Dukes, 2001; Taupp et Wetzel, 2019). Indeed, the invasive *Bosmina coregoni* was found in only a handful (7) of lakes in Eastern Canada. The similar functional space we observed between top and bottom sediments could also have contributed to the stable functional composition observed in the CAPs (Table 3.1b).

Despite the significant species losses observed within lakes between time points (mean richness declined from 15.14 to 13.74 species), country-wide, we noted no net loss in species richness (gamma-diversity), indicating that different species were lost among lakes. While we considered a large geographical region and changes over the past ~150 years, our study highlights that local crustacean species losses, occurring especially in highly impacted lakes, have not yet translated into overall richness losses. Because different species were lost among lakes, our study highlights the differential effects of local stressors at this large continental scale. Nonetheless, our results contrast with global freshwater biodiversity declines (Collen *et al.*, 2014), which might still occur, given time lags between human impacts and species extinction have previously been reported (Essl *et al.*, 2015; Gilbert et Levine, 2013). Delayed biodiversity responses (i.e., relaxation times) to environmental changes can be associated to many mechanisms, including ecosystem degradation and climate change (Essl *et al.*, 2015). A temporal delay between local diversity declines and regional extinctions might also be observed given the metacommunity nature of zooplankton lake communities (Beisner *et al.*, 2006). Because zooplankton have relatively high dispersal potential (Havel et Shurin, 2004) their communities are relatively well connected. As a result, a species once lost may be replaced over time with other more tolerant species occupying the same ecological niche. Although not having translated yet into net losses, local declines in zooplankton diversity should be seen as a warning sign of perturbation to Canadian lakes and relevant to aquatic ecosystem management plans.

3.5.3 Similar spatial homogenisation between past and present

In relation to our third hypothesis, we expected greater spatial homogenization of cladoceran species or functional traits in present times relative to pre-industrial times because of the combined effects of climate change, human activities and the creation of artificial connections between lakes (Lockwood *et al.*, 1997; McGill *et al.*, 2015; Olden *et al.*, 2004). However, our analyses surprisingly revealed that the overall historical and modern cladoceran spatial taxonomic and functional β-diversity were not significantly different (historical = 0.33 both taxonomic and functional, vs. modern = 0.35 both taxonomic and functional). In a previous study of diatom assemblages from 169 lakes in the United States, Winegardner et al. (2017) also found similar spatial β-diversity values between pre-AD 1850 and 2007 time points, aligning with our findings. Our results indicate that habitat homogenization via land use intensification and hydrological alteration did not increase biotic homogenization, independent of human impact class. Instead, species and traits remained as spatially heterogeneous as they were before humans altered the landscape, highlighting the importance of local stressors acting with contrasting regional effects at this large spatial scale. The strong heterogeneous environmental filtering reported across Canadian lakes (Paquette et al. 2022) could thus be driving local communities in different directions, potentially compensating for other homogenizing forces.

3.5.4 Non-significant Increase in temporal turnover under high human impact

In our final hypothesis, we expected greater temporal turnover under higher human impact. We observed that taxonomic and functional temporal turnover only demonstrated non-significant increasing trends under high human impact, thereby providing weak support for our prediction (taxonomic: 0.60 low vs. 0.72 high; functional: 0.33 low vs. 0.37 high; Table S2 in Annexe S). This result aligns with the compositional and α-diversity patterns, indicating that some degree of temporal changes occurred in individual lake ecosystems due to anthropogenic stressors, although these changes have not translated into a continental pattern of species losses or spatial homogenization. Overall, functional composition remained more stable than taxonomic turnover over time, with no significant difference between trait losses or gains. Tsikopoulou et al. (2021) similarly observed stability in functional composition of marine benthic communities over time, despite declines in taxonomic and functional α-diversity, indicating ecosystem resilience to environmental stressors.

When relating taxonomic and functional temporal turnover to human activities, we found that urban land use was the most important factor associated with temporal change in species composition (Figures 3.5 and 3.6). Very small fractions of urban land use in the watershed were responsible for separating lakes between those that experienced greater species and trait temporal change from those that remained more stable (4% and 12% of urban land use the watershed, respectively). As hypothesized by Winegardner et al. (2017), the effect of very low levels of land use on β-diversity might come from watershed development patterns. Indeed, as humans establish in a new region, shorelines are often developed first, affecting riparian and littoral vegetation, while the rest of the watershed remains intact longer (Kaufmann *et al.*, 2014). Thus, especially in urban regions, humans might establish earlier near the lake, affecting species composition despite very low proportional use of the overall watershed area. These results thus indicate that even small changes in human land use can contribute to important changes in zooplankton composition, with consequences potentially extending to cascading effects on lake food webs. Future work analyzing different sizes of rings of land use types around lakes will be essential to further these results on the effect of urban land use on temporal composition changes. However, a more in-depth analysis of sediment temporal dynamics would be necessary to fully evaluate the effect of human impact on temporal β-diversity.

3.6 Conclusions

Our paleolimnological assessment of freshwater cladoceran assemblages over large temporal and spatial scales across Canada revealed taxonomic and functional patterns in composition and diversity over the Industrial period. Although the country-wide diversity remained stable, we observed significant changes in species composition over time, especially in highly impacted lakes, translating into overall local α-diversity losses across our 101 study lakes. However, contrary to our initial expectation, it appears that species function in the ecosystem remained stable, and that spatial homogenization did not increase over time, despite lakes being subject to a myriad of anthropogenic stressors. We also found little support for our temporal β-diversity prediction with only a non-statistically significant trend towards increased temporal turnover under higher human impact. Our results highlighted the important role of watershed land use in shaping diversity, with urban regions showing higher temporal turnover, while reduced taxonomic α-diversity was observed in agriculture and pasture dominated sites. Overall, these results demonstrate the importance of combining taxonomic and functional dimensions, and both α- and β-diversity to help answer important questions about how and where Canadian lakes have changed over the Anthropocene. An essential next research step will be to disentangle the effects of climate change from those arising from human impact in the watersheds by combining analyses of lake-specific climate information, with historical land use time series and cladoceran subfossil temporal records.

CONCLUSION

3.7 Objectifs généraux

Les écosystèmes lacustres sont des hauts lieux de biodiversité et fournissent de nombreux services écosystémiques. Cependant, les perturbations environnementales d'origine anthropique façonnent actuellement les communautés aquatiques du monde entier. Alors que le Canada détient la troisième plus grande réserve d'eau douce renouvelable au monde (Statistique Canada, 2017), une perspective nationale sur la santé de nos lacs n'avait pas été considérée avant la mise en place de l'échantillonnage pancanadien des lacs du réseau LakePulse. Avec ce projet il a été possible de répondre à la question pressante : quel est l'état de santé des lacs canadiens? En tant que niveau trophique clé, médian les ressources ascendantes et descendantes, le zooplancton est un excellent indicateur de qualité d'eau et donc de santé des lacs. Dans ce contexte, mon projet de doctorat visait à déterminer les facteurs influençant la structure et la fonction des communautés de zooplancton sous une large échelle spatiale et temporelle. Cette thèse présente ainsi la première étude standardisée du zooplancton à l'échelle du Canada, le pays avec la plus grande quantité de lacs mondialement. Le premier objectif de cette thèse était de caractériser la biogéographie du zooplancton à travers de Canada et de mettre en évidences les régions de haute diversité. Ce chapitre offre la première analyse des traits fonctionnels du zooplancton canadien. Nous avons également exploré les gradients géographiques et les mécanismes associés façonnant la distribution du zooplancton à différentes échelles spatiales. Dans le deuxième chapitre, nous avons évalué les effets d'une myriade de variables environnementales sur la composition et la diversité du zooplancton. De plus, l'effet combiné de la qualité de l'eau, de la morphométrie des lacs, de l'utilisation des terres et de la prédation des poissons sur la diversité taxonomique et fonctionnelle du zooplancton à l'échelle continentale a été examiné pour la première fois. En ciblant plusieurs hypothèses basées sur la littérature, nous avons testé des relations clés entre l'environnement et la structure du zooplancton à l'échelle continentale. Finalement, l'objectif du troisième chapitre de cette thèse était de déterminer comment les communautés de zooplancton ont changé dans les lacs canadiens depuis l'ère préindustrielle en relation aux activités humaines. Nous avons exploré cette question via la diversité bêta temporelle, un indice de diversité émergent, et d'autant plus lorsqu'analysé sous une approche fonctionnelle. Ce chapitre présente par ailleurs la première analyse de la diversité bêta fonctionnelle temporelle du zooplancton.

Ensemble, les trois chapitres de cette thèse offrent l'examen le plus exhaustif des changements spatiaux et temporels du zooplancton à l'échelle continentale. Avec une approche standardisée combinant les dynamiques taxonomiques et fonctionnelles du zooplancton, plus d'une quarantaine de variables environnementales dans 624 lacs à travers le Canada, ainsi que les changements dans la structure des communautés depuis l'ère préindustrielle, ce travail représente une étape importante dans l'amélioration de la compréhension généralisée des impacts anthropiques sur la structure et la fonction du zooplancton des lacs à l'échelle continentale.

3.8 Importance structurante des bassins versants continentaux

Le Canada comprend six bassins versants continentaux, lesquels délimitent le territoire où les eaux s'écoulent vers différents océans, mers ou golfs. Cette thèse a d'abord mis en évidence l'importance de ces bassins continentaux pour structurer la communauté de zooplancton canadienne. En effet, nous avons démontré dans le premier chapitre que la composition taxonomique et fonctionnelle des communautés était davantage structurée par les bassins continentaux que par écozones, une division à plus petite échelle basée sur des gradients environnementaux. Nous avons également relevé un important gradient longitudinal de diversité et de composition à travers ces bassins continentaux, où les communautés de l'Est canadien étaient plus diverses, mais moins uniques. Ces résultats ont été attribués à une combinaison de facteurs climatiques (direction des vents dominants et températures nordiques plus froides) et géologiques (isolation physique créée par les Rocheuses canadiennes).

L'importance des bassins continentaux a également été notée dans le deuxième chapitre, où une grande hétérogénéité spatiale a été observée dans les relations environnement-diversité entre les différentes régions. En effet, l'importance des variables environnementales a grandement varié à travers le large territoire Canadien. Par exemple, les lacs de l'Ouest canadien étaient caractérisés par des lacs profonds et clairs, alors que le centre du Canada contenait des lacs généralement peu profonds avec une plus haute teneur en nutriments et en ions. Ainsi, non seulement les taxons observés et leur fonction différaient entre bassins continentaux (Chapitre I), mais les variables environnementales avaient également une importance hétérogène sur le territoire (Chapitre 2). Les différents paramètres environnementaux ont donc joué des rôles contrastés sur le zooplancton entre les régions, mettant en lumière l'importance de ne pas généraliser les patrons observés à plus petite échelle.

3.9 Prédicteurs environnementaux des communautés de zooplancton

De nombreuses études ont évalué l'effet des facteurs de stress individuels sur les communautés de zooplancton, médiés par des changements dans la qualité de l'eau (par exemple, l'eutrophisation, la salinisation ou les pesticides) (e.g., Gutierrez *et al.*, 2018; Hébert *et al.*, 2021; Moody *et al.*, 2021). Cependant, de plus en plus, ces facteurs interagissent dans les écosystèmes, nécessitant des recherches considérant l'effet d'interactions sur les communautés en milieu naturel (Jackson *et al.*, 2016). Il a également été démontré que la morphométrie des lacs (St-Gelais *et al.,* 2017) et la prédation par le poisson (Gliwicz, 2003) sont d'importants déterminants de la structure ou de la fonction des communautés de zooplancton. Précédemment, aucune étude n'avait investigué l'effet combiné de ces facteurs sur la composition et la diversité du zooplancton, malgré les évidences connues de leur importance individuelle. Ainsi, dans le deuxième chapitre de cette thèse, nous avons mis en évidence une hiérarchie dans l'importance des types de variables environnementales pour le zooplancton, où la morphométrie des lacs était plus critique pour la diversité, alors que la qualité de l'eau influençait davantage la composition des communautés. Étonnamment, nous n'avons observé qu'un effet minime de la prédation par le poisson sur la communauté de zooplancton par rapport aux autres variables. Nos résultats suggèrent donc qu'à l'échelle des bassins continentaux, les variables de prédation pourraient être moins importantes que celles de l'environnement.

3.10 Impact des activités humaines sur le zooplancton

Il existe une forte corrélation entre l'utilisation du sol d'un bassin versant et la qualité de l'eau observée dans un lac (Lee *et al.*, 2009). Ainsi, au-delà des paramètres de qualité d'eau, il est essentiel de tenir compte des différentes activités humaines prenant place autour d'un lac afin d'évaluer proprement le rôle de l'environnement sur une communauté aquatique. Dans cette présente thèse, l'impact de différents types d'utilisation du sol (agriculture, pâturage, prairies aménagées, urbanisation, déforestation et activités minières) a été considéré pour la diversité et la composition du zooplancton (chapitre II) et pour les changements temporels des cladocères depuis l'ère préindustrielle (chapitre III). À travers le Canada, l'agriculture a semblé être la catégorie d'utilisation du sol affectant le plus les communautés de zooplancton. En effet, nous avons observé que les régions agricoles avaient non seulement une diversité fonctionnelle distincte, mais avaient aussi connu une plus grande perte en diversité depuis l'ère préindustrielle.

À l'échelle du Canada, nous avons d'ailleurs observé une réduction de la diversité locale taxonomique et fonctionnelle depuis l'ère préindustrielle, telle que reportée mondialement (Davies *et al.*, 2006). La fraction du bassin versant provenant de l'agriculture ou des pâturages était la catégorie d'utilisation du sol la plus importante pour ces pertes de diversité taxonomique. En termes de composition, les assemblages de cladocères contemporains étaient également structurés par les niveaux d'activité humaine, en particulier dans les lacs fortement impactés. Nous avons d'ailleurs observé que l'urbanisation était le facteur le plus important associé au changement temporel de la composition taxonomique et fonctionnelle des assemblages de zooplancton. À l'échelle écosystémique, ces résultats suggèrent que l'utilisation du sol, et plus particulièrement l'agriculture, le pâturage et l'urbanisation sont des menaces pour l'équilibre des communautés aquatiques. À l'heure actuelle, les lignes directrices sur l'utilisation du sol dans le bassin versant des lacs ne sont donc pas suffisantes pour protéger les écosystèmes d'eau douce.

3.11 L'approche fonctionnelle en écologie des communautés

Une approche combinant les dimensions taxonomiques et fonctionnelles a été utilisée tout au long de cette thèse. Alors que la taxonomie permet une évaluation des dynamiques et des changements à plus fine échelle, l'écologie fonctionnelle concerne davantage la façon dont les espèces interagissent avec leur environnement. À travers les trois chapitres, nous avons généralement observé des réponses plus faibles aux patrons spatiaux (Chapitre I), environnementaux (Chapitre II) et temporels (Chapitre III) des indices fonctionnels par rapport à ceux basés sur la taxonomie. Ces résultats sont probablement dus à la redondance des traits fonctionnels chez le zooplancton (Barnett *et al.,* 2007), et ce particulièrement à cette grande étendue spatiale. Malgré cette redondance, nous avons observé une hétérogénéité spatiale des traits fonctionnels à l'échelle du Canada, avec des communautés fonctionnellement distinctes entre les bassins continentaux (Chapitre I). Cette redondance fonctionnelle a également assuré la résilience de la fonctionnalité globale des cladocères depuis l'ère industrielle nonobstant un changement de composition taxonomique et une perte de diversité en présence d'importants facteurs de stress environnementaux (Chapitre III). Nos résultats suggèrent aussi que la prise en compte des approches taxonomiques et fonctionnelles peut être essentielle pour démêler les schémas biogéographiques de diversité bêta à grande échelle. Dans le premier chapitre, nous avons ainsi démontré pour la première fois que les traits fonctionnels pourraient être plus informatifs que la taxonomie pour identifier les espèces qui contribuent le plus à la diversité bêta, soulignant l'importance d'incorporer des traits fonctionnels dans les plans de conservation.

3.12 Limites et perspectives futures

Malgré l'ampleur de ce projet, certaines limites doivent être prises en considération. D'abord, étant donnée sa portée géographique, un important compromis de l'échantillonnage du réseau LakePulse a été de favoriser le nombre de lacs échantillonnés et la quantité des variables examinées, plutôt que d'examiner un nombre restreint de lacs et de variables sous une perspective plus approfondie. Ainsi, les données du projet ne nous ont pas permis d'examiner les dynamiques saisonnières et spatiales (à l'intérieur d'un même lac) du zooplancton pélagique canadien. Or, il est connu qu'une importante variabilité des communautés puisse avoir lieu entre les saisons (De Senerpont Domis *et al.*, 2013) ou entre les milieux pélagiques et benthiques des lacs (Avois *et al.*, 2000). L'utilisation des carottes de sédiments a toutefois permis de combler en partie cette lacune en intégrant les communautés de cladocères à travers les saisons, l'espace (à l'intérieur d'un même lac) et les années. Éventuellement, une comparaison des données des sédiments de surface et des données pélagiques contemporaines serait nécessaire pour renforcir les liens entre les variables environnementales et les indices de structure des communautés observées au Chapitre 2.

L'incorporation des données de poissons provenant des ministères provinciaux et territoriaux a été un ajout important à la richesse de la base de données collectées par LakePulse.

Cependant, étant seulement de type « présence », ces données ne reflètent que partiellement le potentiel de prédation sur le zooplancton. Idéalement, des données plus complètes de présence-absence, ou de capture par unité d'effort (CPUE) auraient permis d'avoir un portrait plus précis de l'importance de la pression de prédation par le poisson. Dans le futur, des informations sur l'occurrence des espèces de poissons dominantes (Minamoto *et al.*, 2012; Valentini *et al.*, 2009), la biomasse (Takahara *et al.*, 2012), ou au moins la dominance de la position trophique (planctivore ou piscivore) pourraient potentiellement être obtenues avec de l'ADN environnemental qui a été collecté par le réseau LakePulse, permettant ainsi de valider ou non nos observations.

Cette thèse comprend l'évaluation des facteurs spatiaux, environnementaux et temporels influençant les communautés de zooplancton d'une envergure incomparable. Il toutefois est à noter que d'autres facteurs peuvent influencer ou régir la communauté de zooplancton, tels que les changements climatiques (Vadadi-Fülöp *et al.*, 2012), les espèces exotiques invasives (Kelly *et al.*, 2013), ou les changements de couverture en macrophytes de lacs (Jeppesen *et al.*, 1998). Cependant, ces éléments n'ont pas été analysés dans cette présente thèse, étant hors des objectifs principaux de la recherche. Éventuellement, il serait tout de même intéressant d'évaluer si ces facteurs jouent également un rôle important sur la structure des communautés de zooplancton à l'échelle continentale.

Bref, en utilisant une méthode combinant différentes dimensions de diversité, des approches à la fois taxonomiques et fonctionnelles, ainsi que des analyses statistiques de pointe, cette thèse souligne l'importance du zooplancton comme indicateur de l'état de santé des lacs canadiens. En soulevant l'importance de la qualité de l'eau et de l'utilisation du sol sur la composition et la diversité taxonomique et fonctionnelle du zooplancton, cette thèse soutient que davantage d'efforts de conservation seront nécessaires pour assurer la pérennité des services écosystémiques offerts par les lacs canadiens dans le contexte actuel d'anthropisation de l'environnement. Au final, il est évident que d'avantage d'études doivent également être menées pour avancer la compréhension de l'impact grandissant des activités humaines sur les écosystèmes aquatiques en général.

ANNEXE A

HUMAN IMPACT INDEX

Human impact was assessed using the land use types (urban, mines, agriculture, pasture, recent clear-cuts and natural landscape) in the watershed of each lake. Human impact classes were created based on the threshold values of Jenks natural break classification independently for each ecozone (Jenks et Caspall, 1971), so that the threshold values in HI classes is different among ecozone.

ANNEXE B

ZOOPLANKTON SAMPLING

At the deepest point in each lake, we collected an integrated water column zooplankton samples using a 100µm mesh Wisconsin net (net radius = 10cm, length = 100cm), with a collection bucket (100µm) attached to the end. The net was hauled vertically from 1-m above the sediments to the lake surface. When lake depth was less than 6-m, additional vertical hauls from 1-m above sediments were taken to increase the volume sampled (to a minimum of 160L in total). Zooplankton were anesthetized with CO_2 (Alka-Seltzer) and preserved in ethanol (final concentration approximately 70%). Samples were then stored at room temperature and sent to BSA Environmental Services (Ohio, U.S.A.) for species-level identification using a dissecting microscope (100x to 400x magnification). For each sample, at least 200 individuals of the most abundant species were counted, up to a total of 1000 individuals. Lakes wherein total abundance was < 100 individuals were removed from the dataset (n =10).

ANNEXE C

LAKE CHARACTERISTICS

Table C.1. Minimum; maximum and (mean) values of lake characteristics, as well as number of lakes by ecozone (a) and continental basin (b). Regions are listed from west to east.

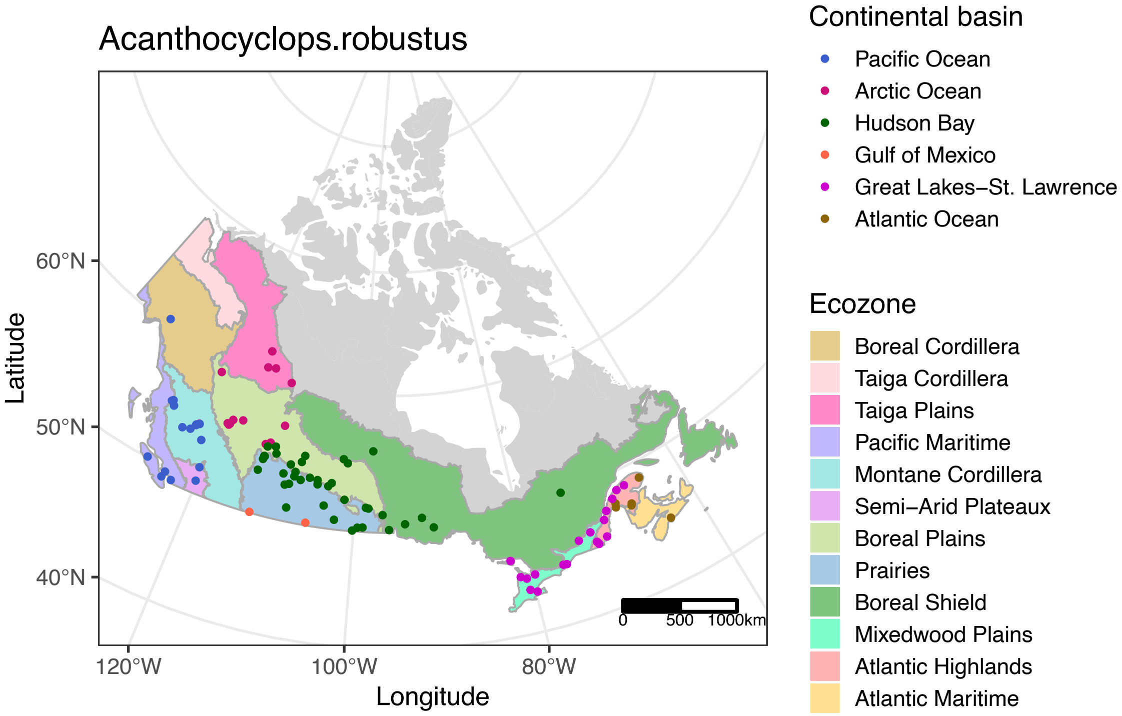
(a) ecozone	Latitude	Longitude	Max depth (m)	Area (km²)	Human impact	Number of lakes
All	43.11; 68.35 (50.64)	-140.60 ; -52.77 (-99.14)	0.65; 150.00 (13.79)	0.01; 99.03 (5.73)	0.00; 0.91 (0.22)	624
Boreal Cordillera	57.85; 63.81 (60.62)	-140.67; -127.56 (-132.83)	0.90; 150.00 (30.20)	0.11; 91.13 (11.21)	0.00; 0.72 (0.05)	30
Taiga Cordillera	64.65; 64.85 (64.74)	-138.39; -138.35 (-138.37)	1.40; 5.20 (3.30)	0.12; 1.29 (0.54)	0.00; 0.03 (0.02)	3
Taiga Plains	59.53; 68.35 (64.25)	-134.92; -111.85 (-124.97)	0.65; 21.60 (4.28)	0.05; 35.66 (2.18)	0.00; 0.46 (0.05)	22
Pacific Maritime	48.38; 56.05 (50.55)	-130.15; -122.02 (-125.21)	2.00; 138.00 (25.7)	0.07; 65.27 (4.43)	0.00; 0.97 (0.23)	69
Montane Cordillera	49.25; 55.33 (53.11)	-126.92; -115.24 (-122.98)	1.80; 94.00 (16.20)	0.11; 68.65 (3.79)	0.00; 0.59 (0.10)	67
Semi-Arid Plateaux	49.29; 51.65 (50.18)	-122.88; -119.23 (-120.22)	3.40; 75.00 (24.48)	0.11; 29.03 (4.73)	0.01; 0.34 (0.09)	33
Boreal Plains	50.47; 58.82 (53.68)	-122.90; -97.41 (-109.54)	1; 42.00 (6.22)	0.12; 94.82 (9.97)	0.00; 0.81 (0.33)	69
Prairies	49.00; 53.92 (51.59)	-113.75; -97.65 (-107.84)	0.75; 21.00 (4.10)	0.01; 81.19 (7.52)	0.00; 0.89 (0.48)	67
Boreal Shield	44.92; 56.64 (48.59)	-102.07; -52.77 (-76.17)	1.10; 66.00 (15.80)	0.05; 69.77 (5.22)	0.00; 0.91 (0.16)	85
Mixedwood Plains	43.11; 46.80 (44.7)	-83.11; -71.39. (-78.97)	1.00; 41.00 (9.19)	0.09; 69.42 (5.12)	0.00; 0.93 (0.34)	53
Atlantic Highlands	45.03; 48.80 (46.98)	-72.67; -64.58 (-69.47)	1.10; 85.00 (13.62)	0.10; 99.03 (5.56)	0.00; 0.42 (0.12)	63
Atlantic Maritime	43.60; 47.58 (45.28)	-67.66; -60.01 (-64.26)	1.04; 44.00 (8.48)	0.10; 58.77 (3.44)	0.00; 0.88 (0.22)	63

ANNEXE D

DISTRIBUTION MAPS OF 90 TAXA

Figure D.1 Distribution map of 90 crustacean zooplankton taxa across 624 Canadian lakes. Lakes are contoured by ecozone and coloured by continental basin. The maps were created using Canada Atlas Lambert projection (NAD83 CSRS).

Acanthocyclops robustus
Acanthodiaptomus denticornis
Acroperus harpae
Aglaodiaptomus clavipes
Aglaodiaptomus forbesi
Aglaodiaptomus leptopus
Aglaodiaptomus spatulocrenatus
Alona affinis
Alona costata
Alona guttata
Alona intermedia
Alona quadrangularis
Alonella acutirostris
Alonella nana
Bosmina longirostris
Camptocercus sp
Ceriodaphnia lacustris
Ceriodaphnia quadrangula
Chydorus sphaericus
Cyclops columbianus
Cyclops scutifer
Daphnia ambigua
Daphnia catawba
Daphnia dentifera
Daphnia dubia
Daphnia galeata mendotae
Daphnia longiremis
Daphnia magna
Daphnia middendorffiana
Daphnia parvula
Daphnia pulicaria
Daphnia retrocurva
Daphnia similis
Daphnia thorata
Diacyclops navus
Diacyclops thomasi
Diaphanosoma birgei
Diaphanosoma brachyurum
Dunhevedia crassa
Epischura lacustris
Epischura nevadensis
Epischura nordenskioldi
Ergasilus spp
Eubosmina coregoni
Bosmina longispina
Eubosmina tubicen
Eucyclops elegans
Eucyclops pectinifer
Eurycercus spp
Graptoleberis testudinaria
Harpacticoida
Hesperodiaptomus arcticus
Hesperodiaptomus eiseni
Hesperodiaptomus franciscanus
Hesperodiaptomus kenai
Hesperodiaptomus nevadensis
Heterocope septentrionalis
Holopedium glacialis
Ilyocryptus spp
Latona sp
Leptodiaptomus ashlandi
Leptodiaptomus minutus
Leptodiaptomus nudus
Leptodiaptomus pribilofensis
Leptodiaptomus sicilis
Leptodiaptomus siciloides
Leptodiaptomus tyrrelli
Limnocalanus macrurus
Macrocyclops albidus
Macrothrix sp
Mesocyclops americanus
Mesocyclops edax
Microcyclops spp
Moina spp
Onychodiaptomus hesperus
Onychodiaptomus singuienus
Orthocyclops modestus
Ostracoda
Picripleuroxus denticulatus
Pleuroxus procurvus
Polyphemus pediculus
Scapholeberis spp
Senecella calanoides
Sida crystallina
Simocephalus spp
Skistodiaptomus oregonensis
Skistodiaptomus pallidus
Skistodiaptomus pygmaeus
Skistodiaptomus reighardi
Tropocyclops prasinus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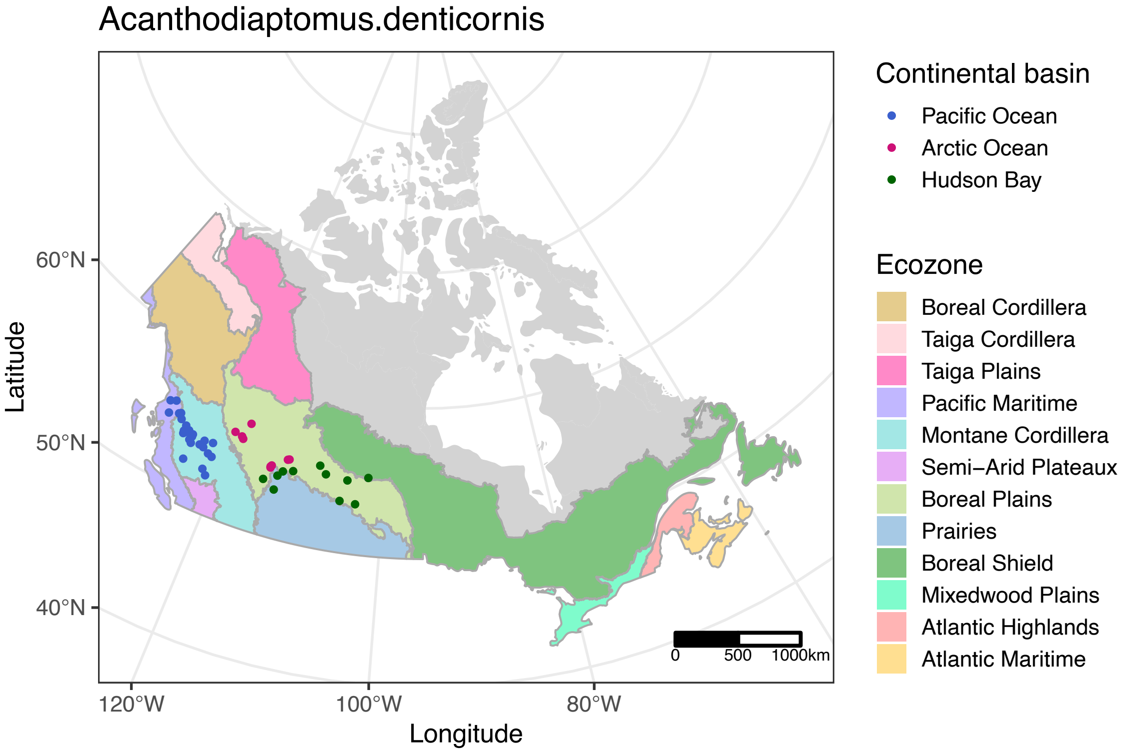
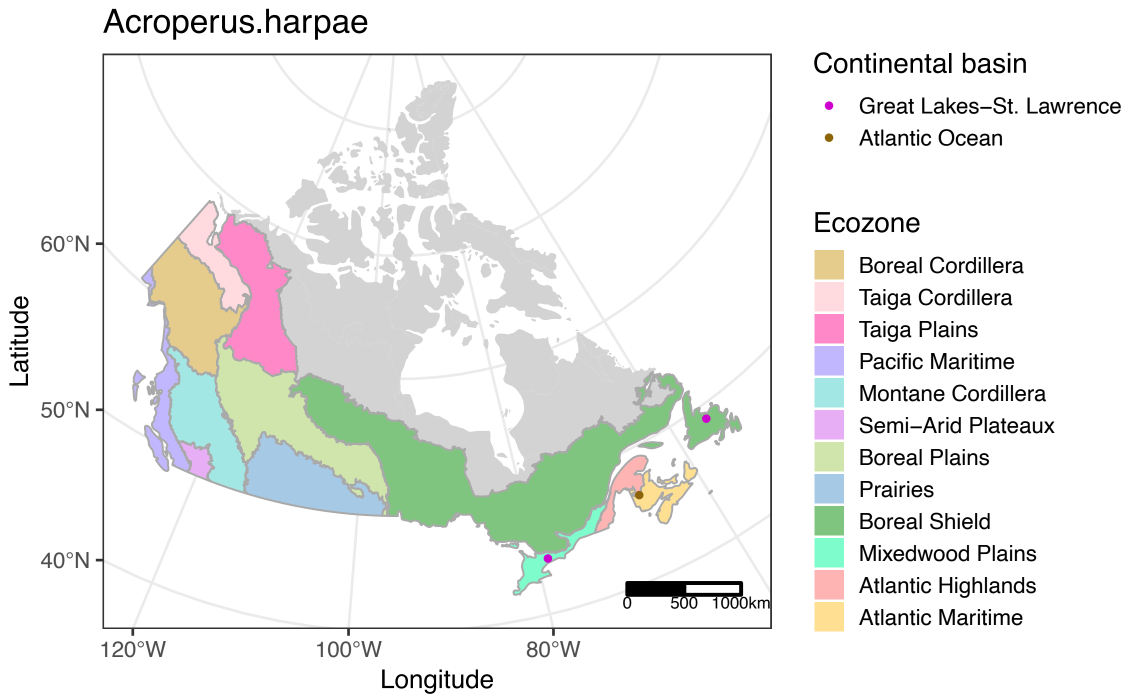
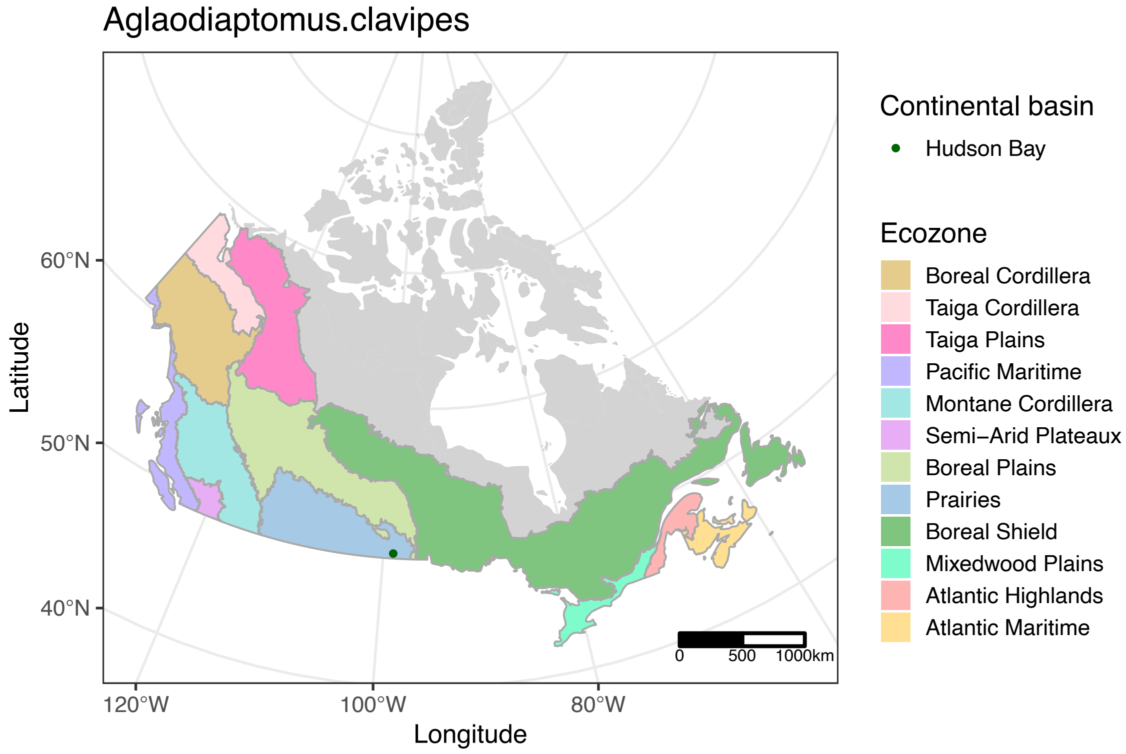
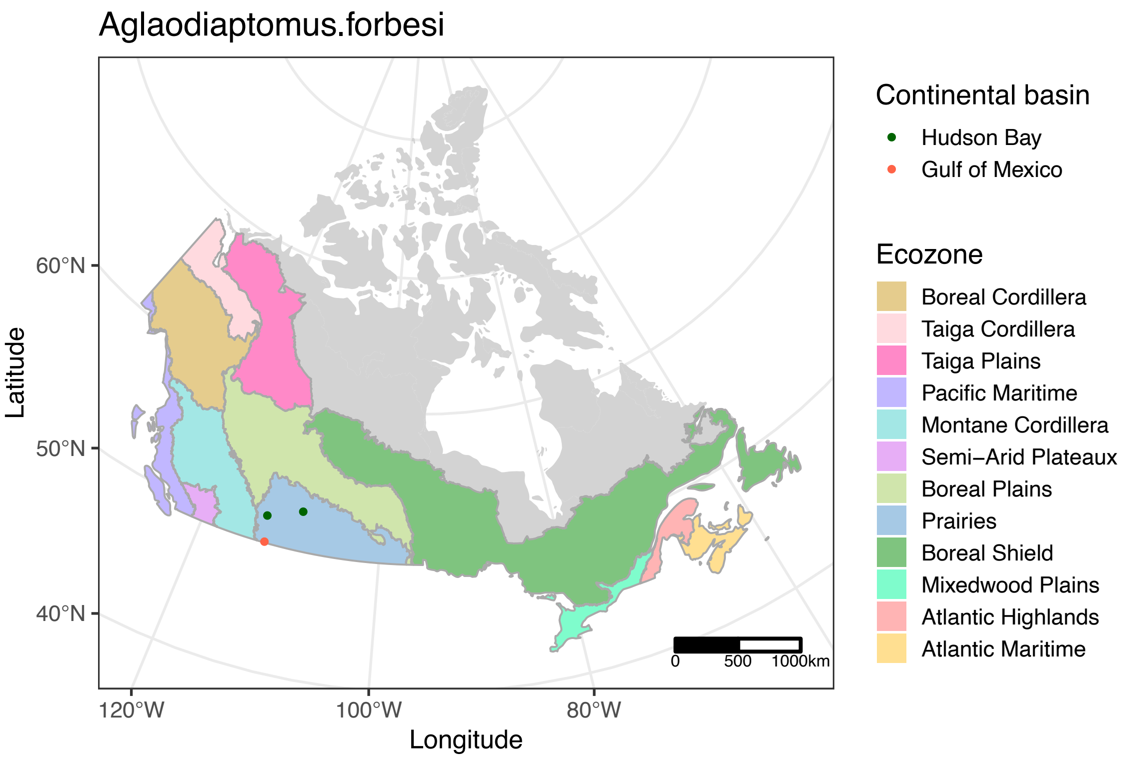

Acanthodiaptomus.denticornis


Acroperus.harpae
Latitude
60°N
50°N
40°N
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Aglaodiaptomus.clavipes
Latitude
60°N
50°N
40°N
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
● Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Aglaodiaptomus.forbesi
Continental basin
Hudson Bay
Gulf of Mexico
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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50°N
40°N
Latitude
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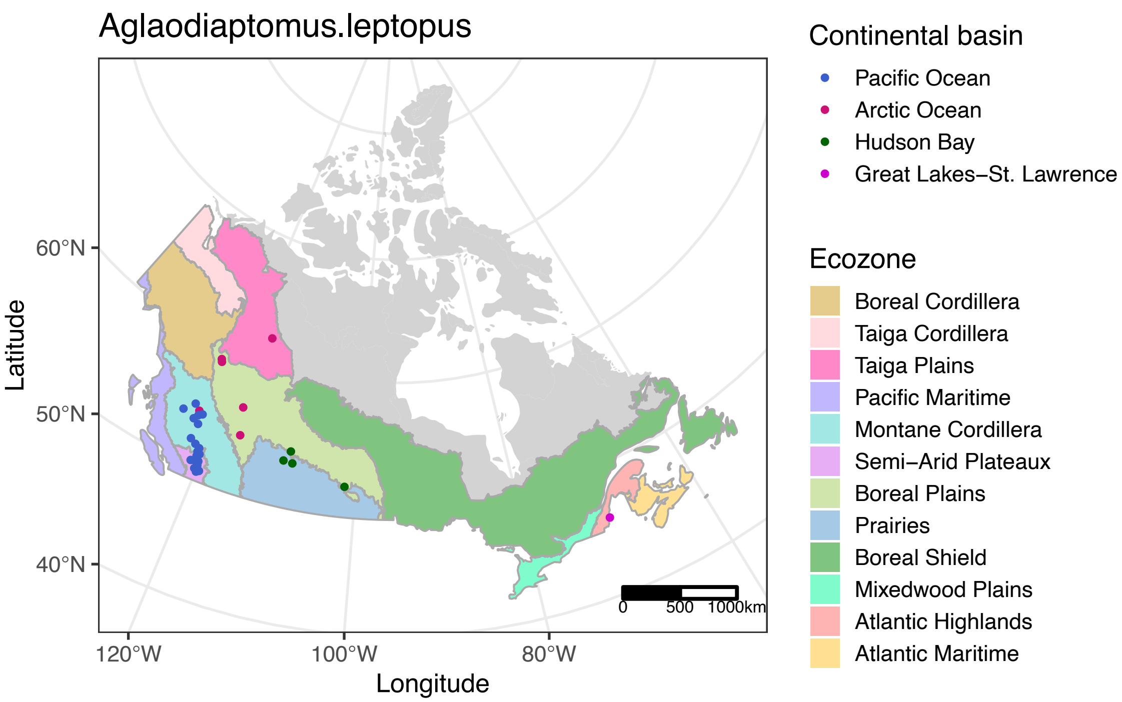
100°W
80°W
Longitude
0
500
1000km


Aglaodiaptomus.leptopus
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
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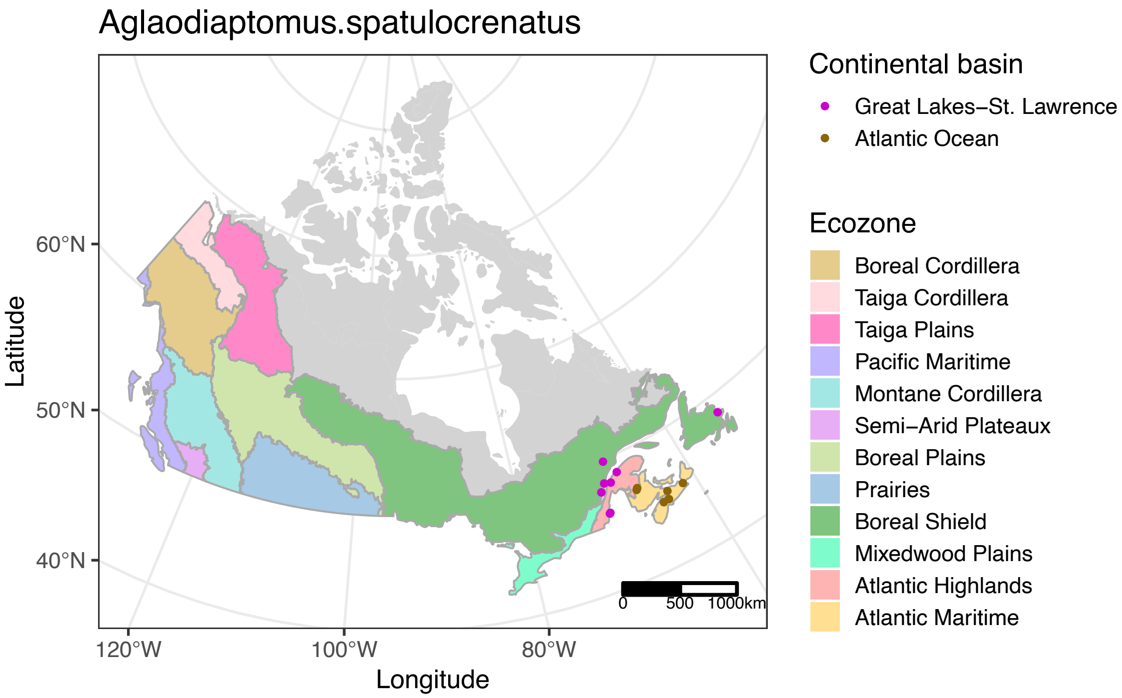
100°W
80°W
Longitude
0
500
1000km


Aglaodiaptomus.spatulocrenatus
Continental basin
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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40°N
Latitude
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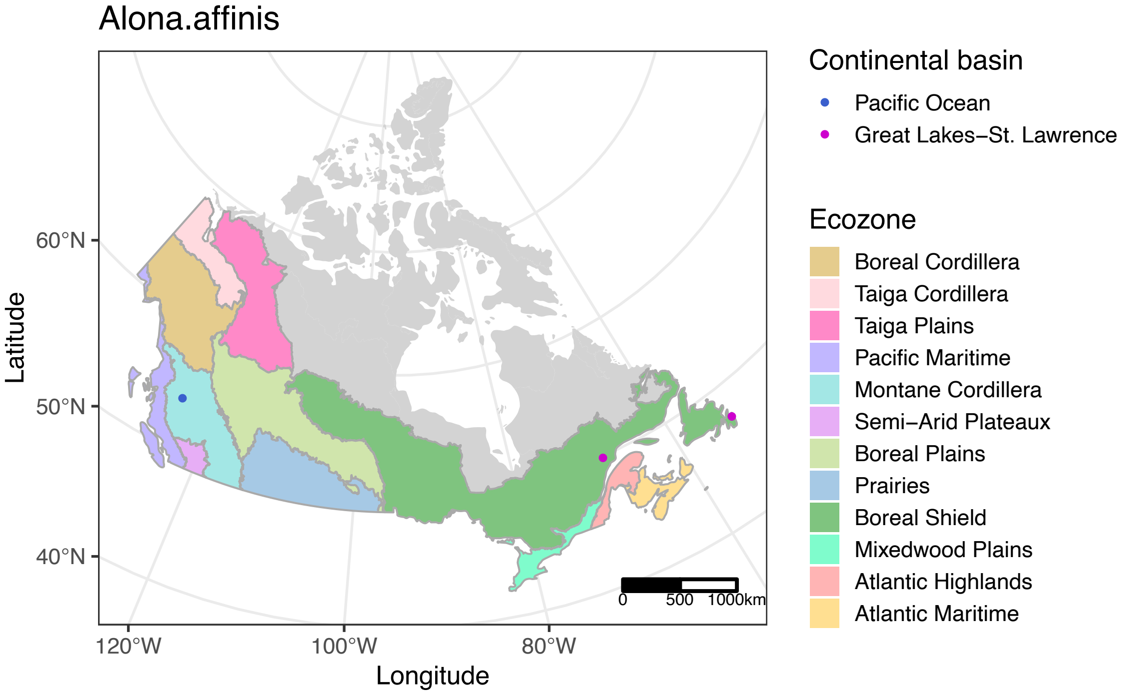
100°W
80°W
Longitude
0
500
1000km


Alona.affinis
Continental basin
Pacific Ocean
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
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Latitude
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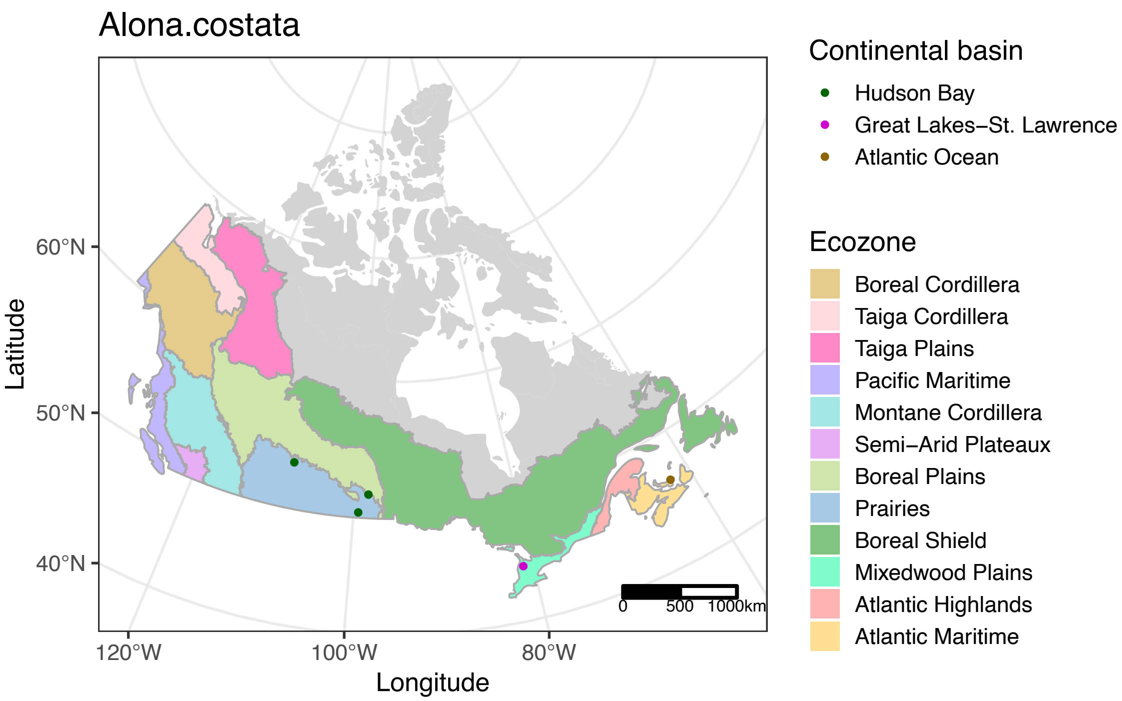
1000km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Latitude
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100°W
80°W
Longitude
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1000km
Continental basin
● Hudson Bay
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
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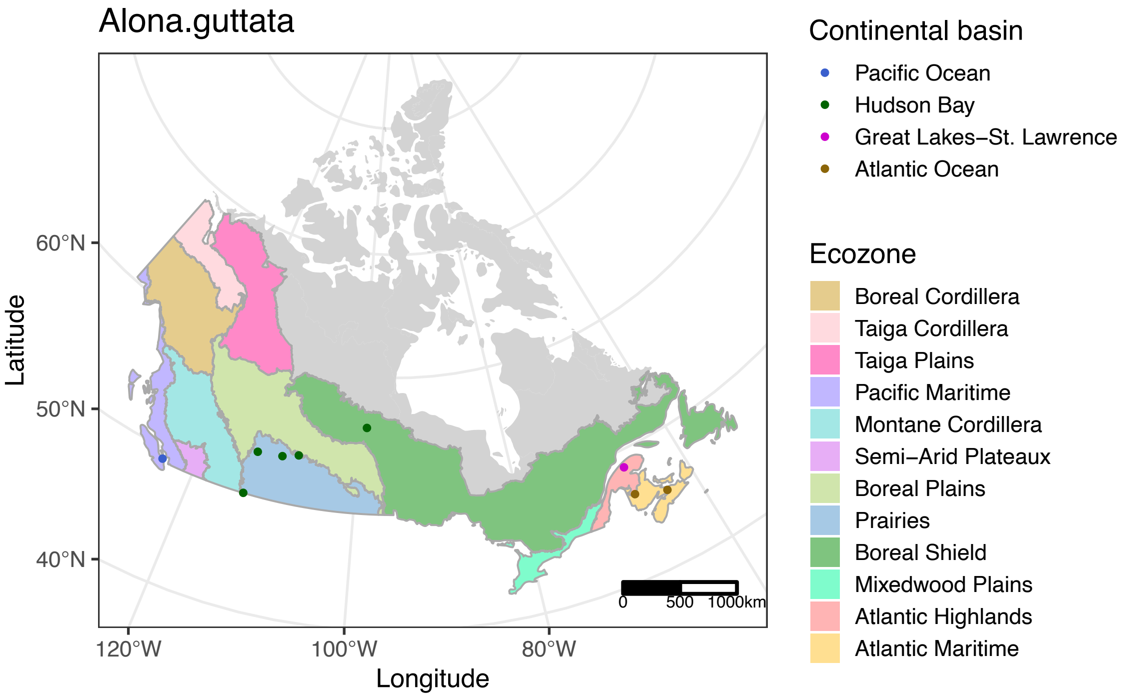
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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60°N
50°N
40°N
Latitude
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100°W
80°W
Longitude
0
500
1000km
Continental basin
● Pacific Ocean
● Hudson Bay
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
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Montane Cordillera
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Prairies
Boreal Shield
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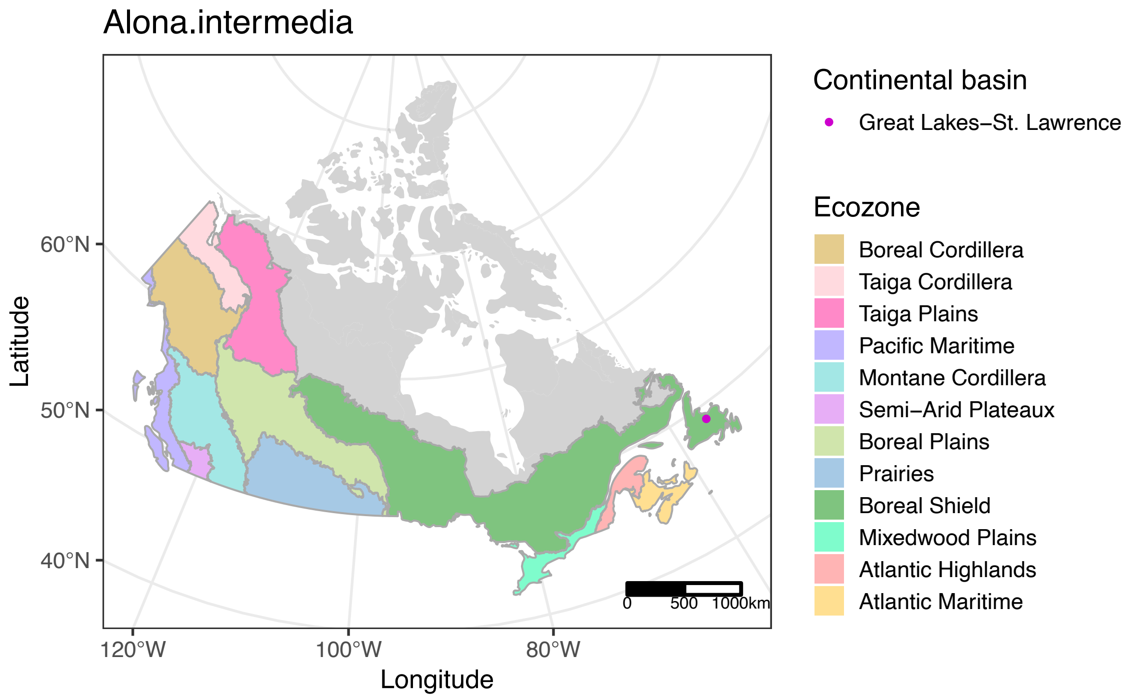
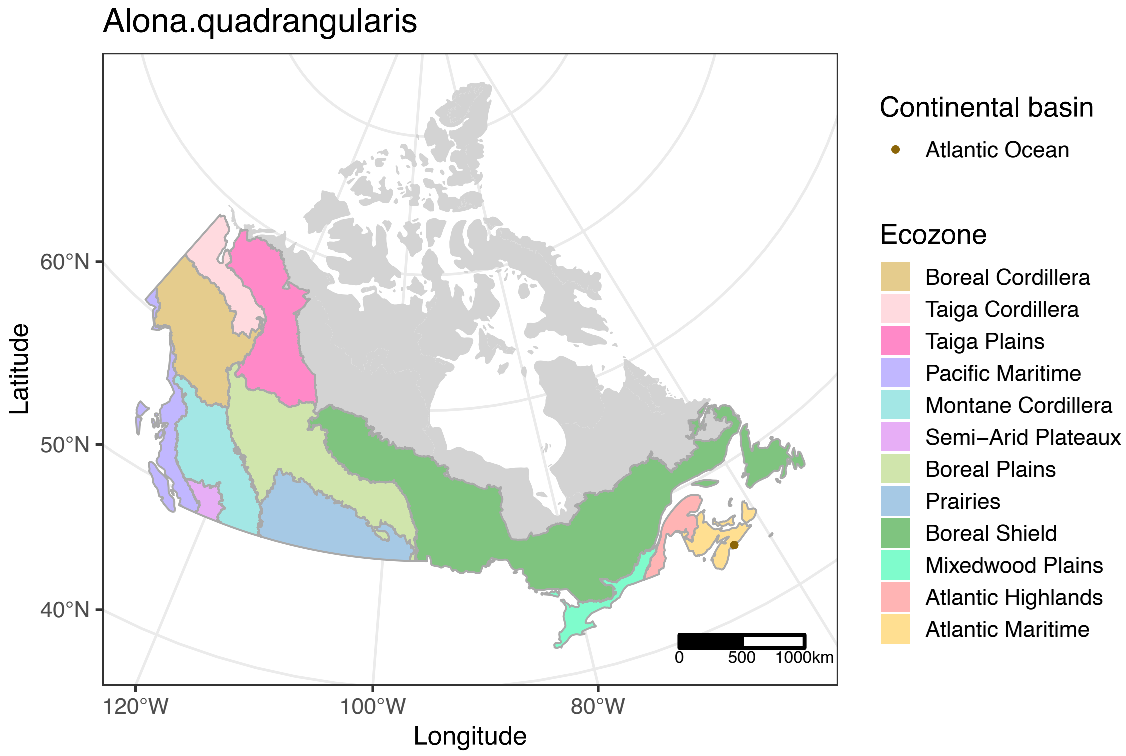
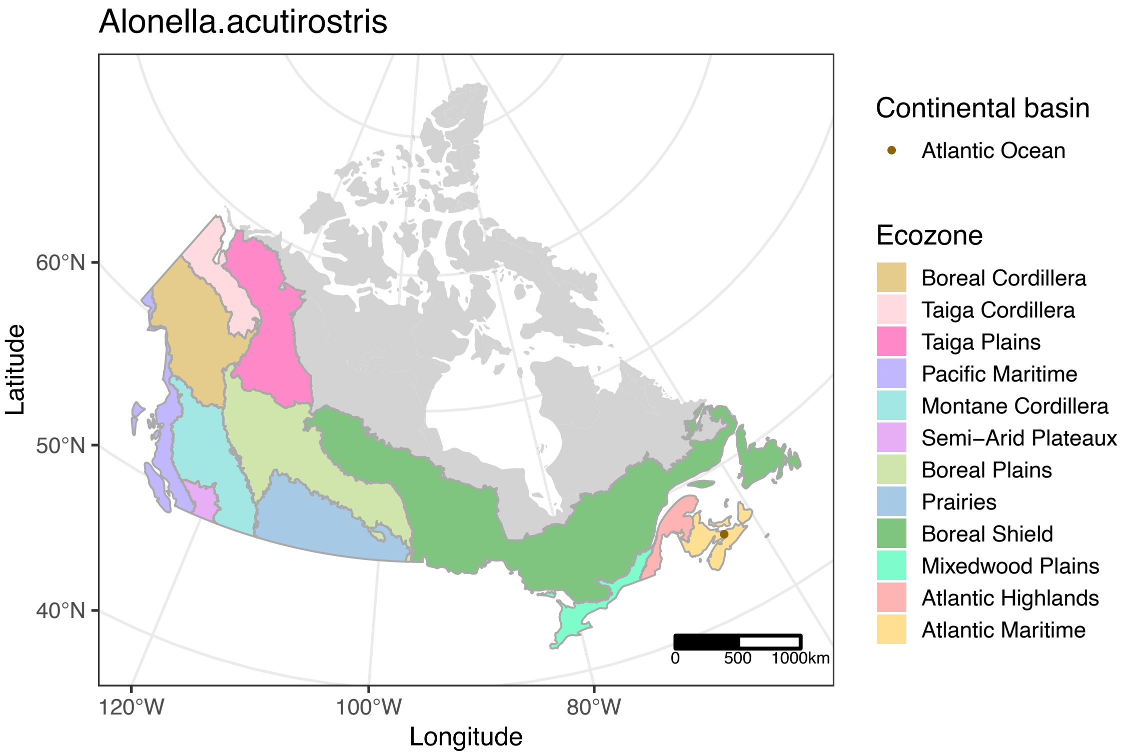
Atlantic Maritime



Alona.intermedia



Alona.quadrangularis


Alonella.acutirostris
Continental basin
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
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Latitude
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100°W
80°W
Longitude
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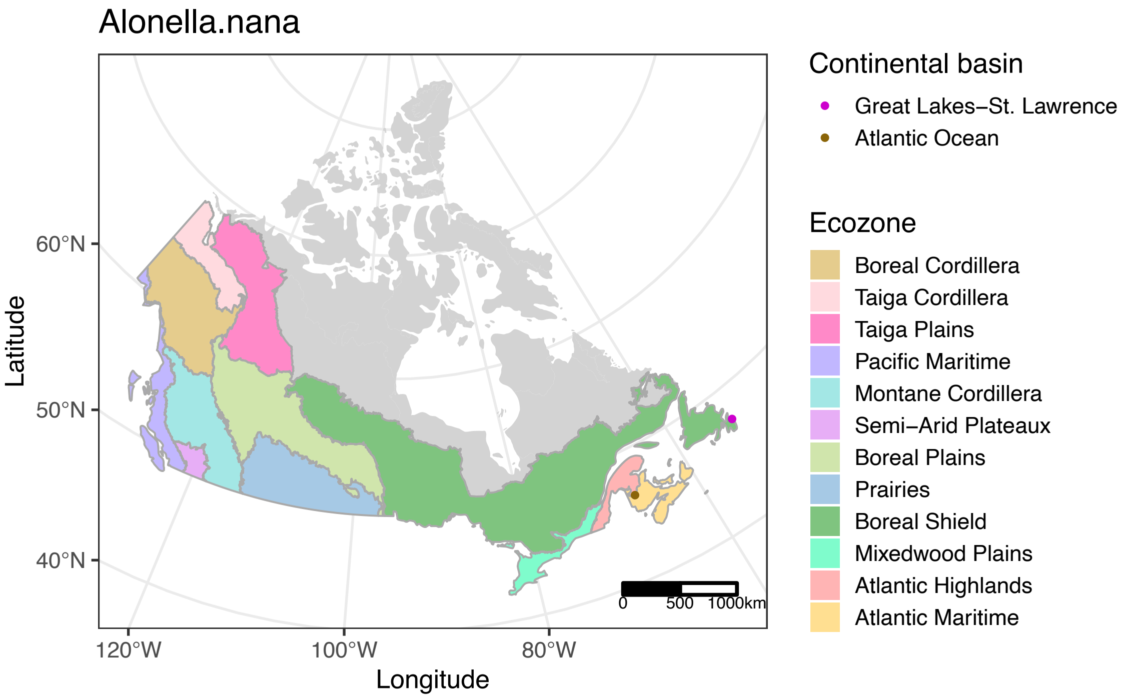
Alonella.nana
Continental basin
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
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50°N
40°N
Latitude
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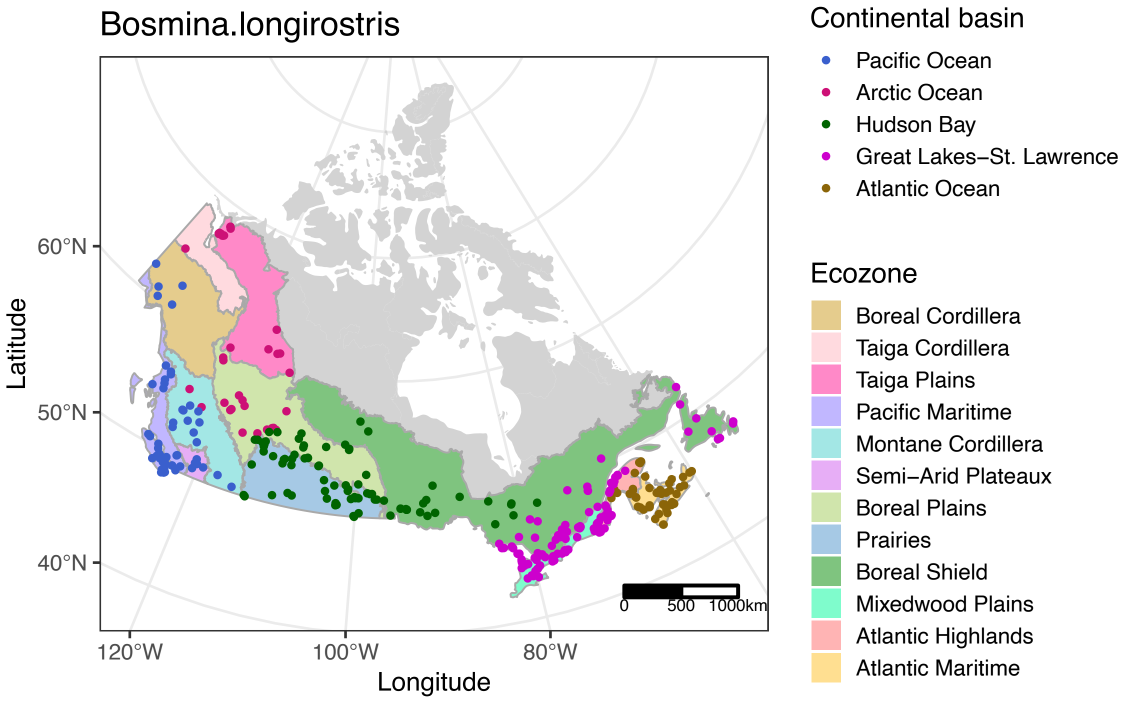
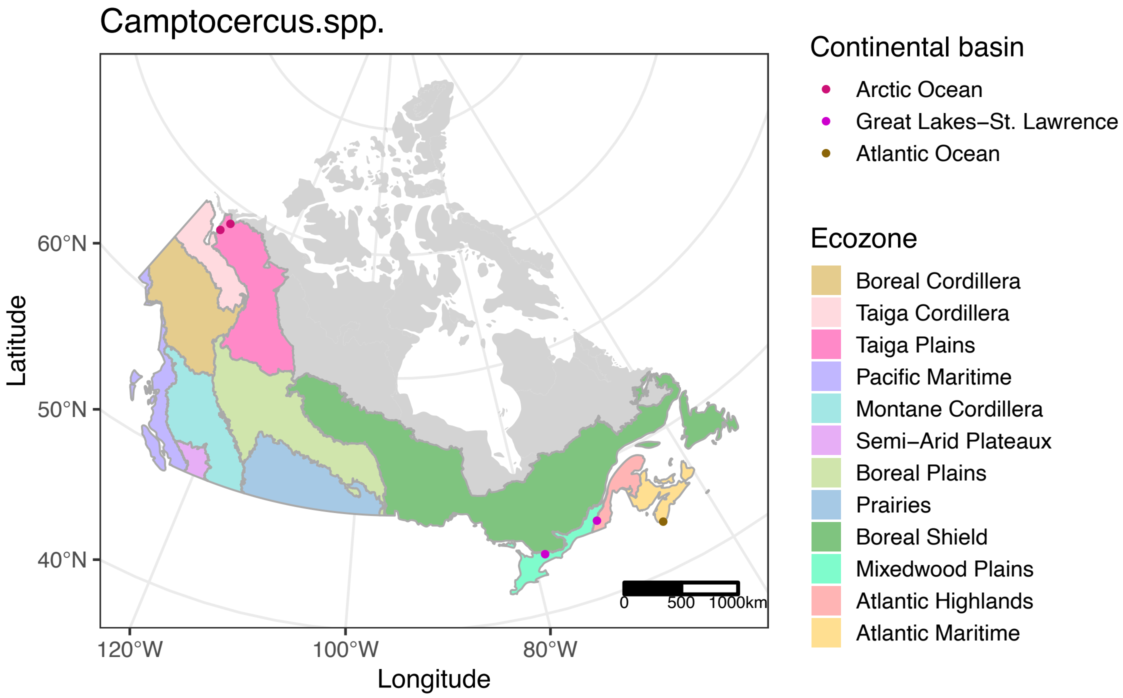
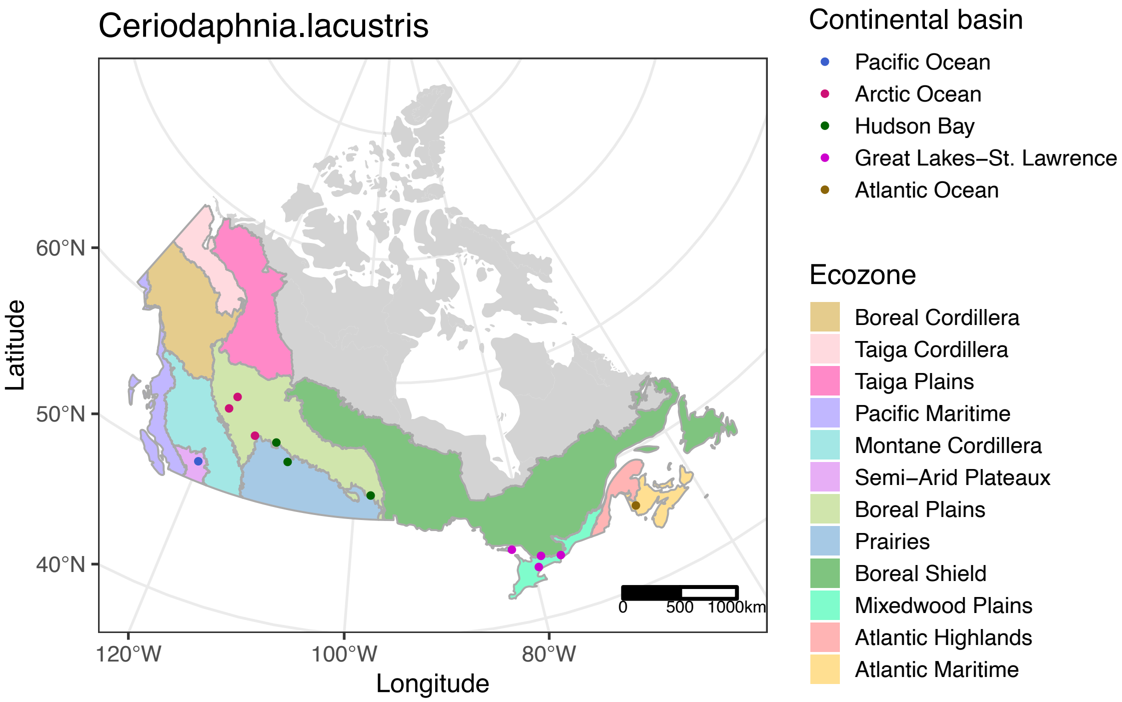
Longitude
0
500
1000km


Bosmina.longirostris


Camptocercus.spp.


Ceriodaphnia.lacustris
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
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Latitude
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Longitude
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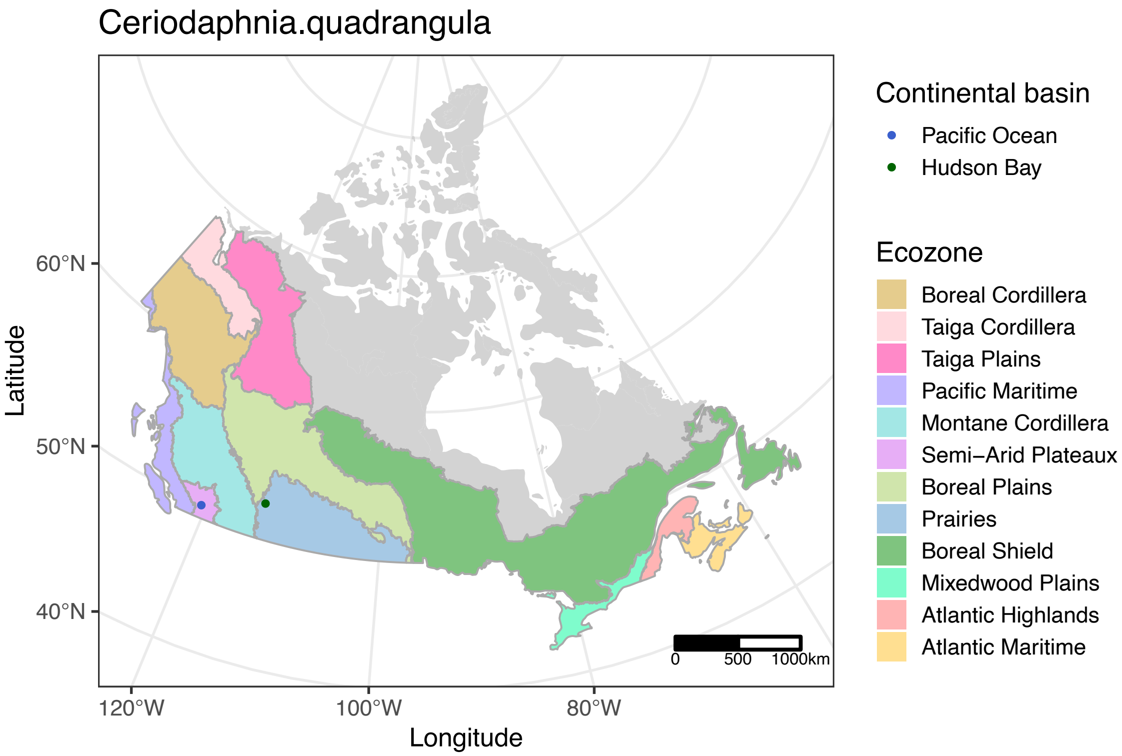
Ceriodaphnia.quadrangula
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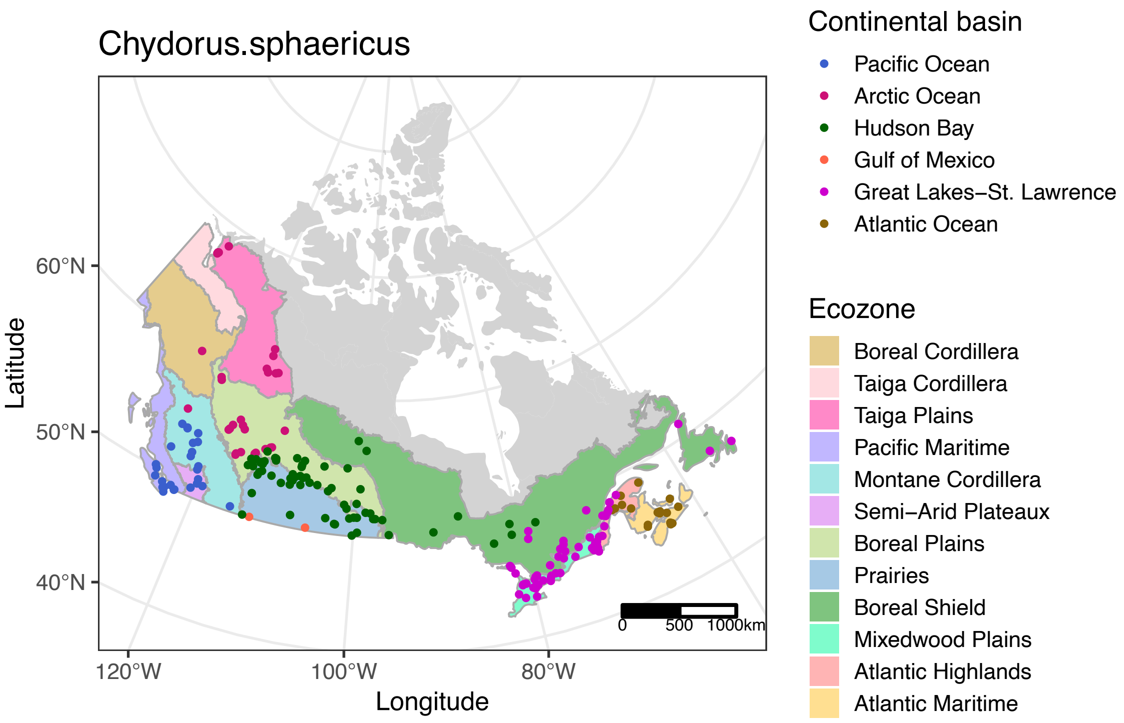
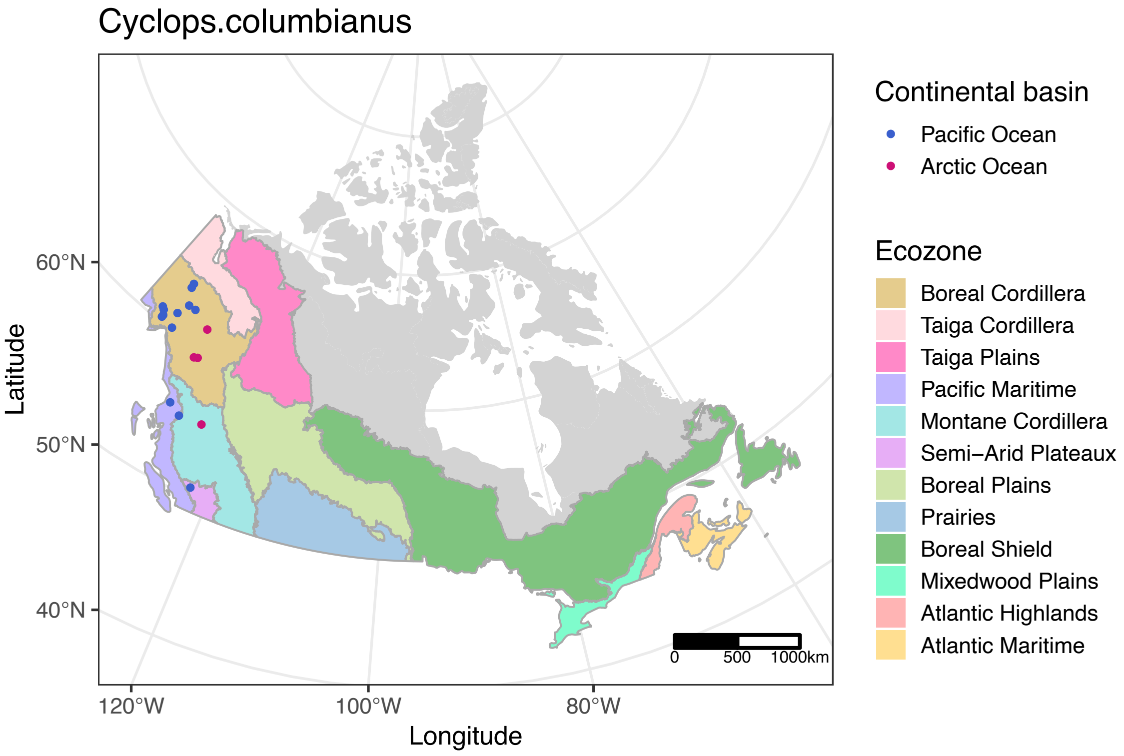
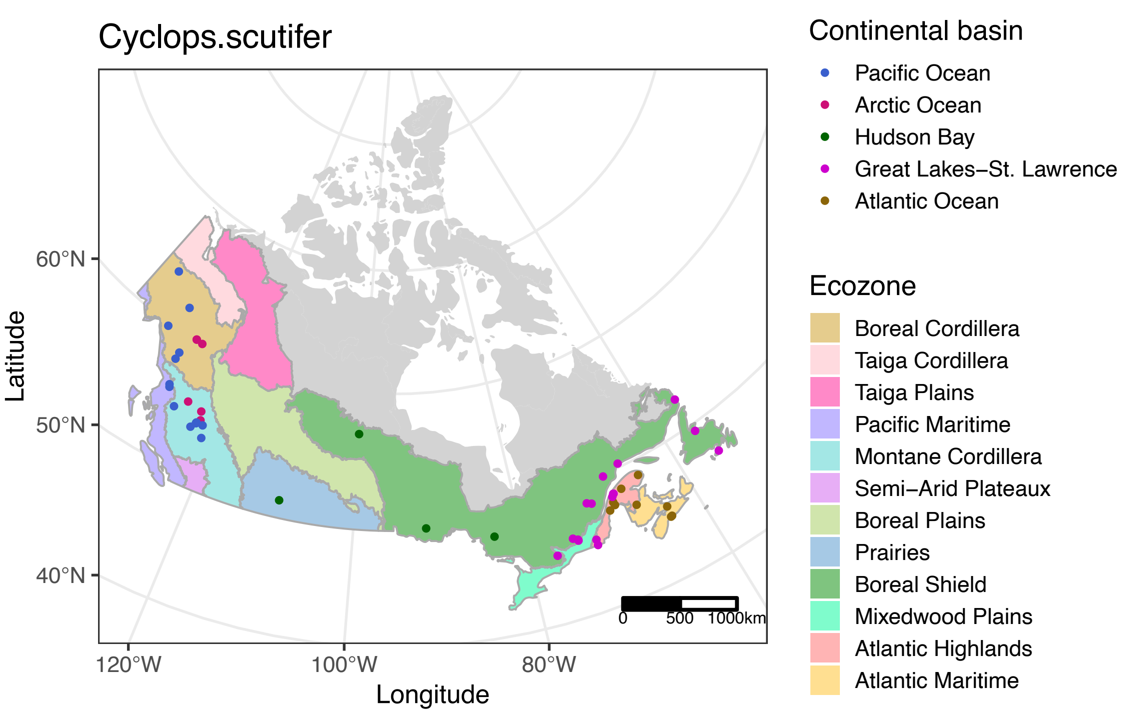
Pacific Ocean
Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km


Chydorus.sphaericus
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Gulf of Mexico
Great Lakes−St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi−Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km


Cyclops.columbianus
Continental basin
Pacific Ocean
Arctic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi−Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km


Cyclops.scutifer
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
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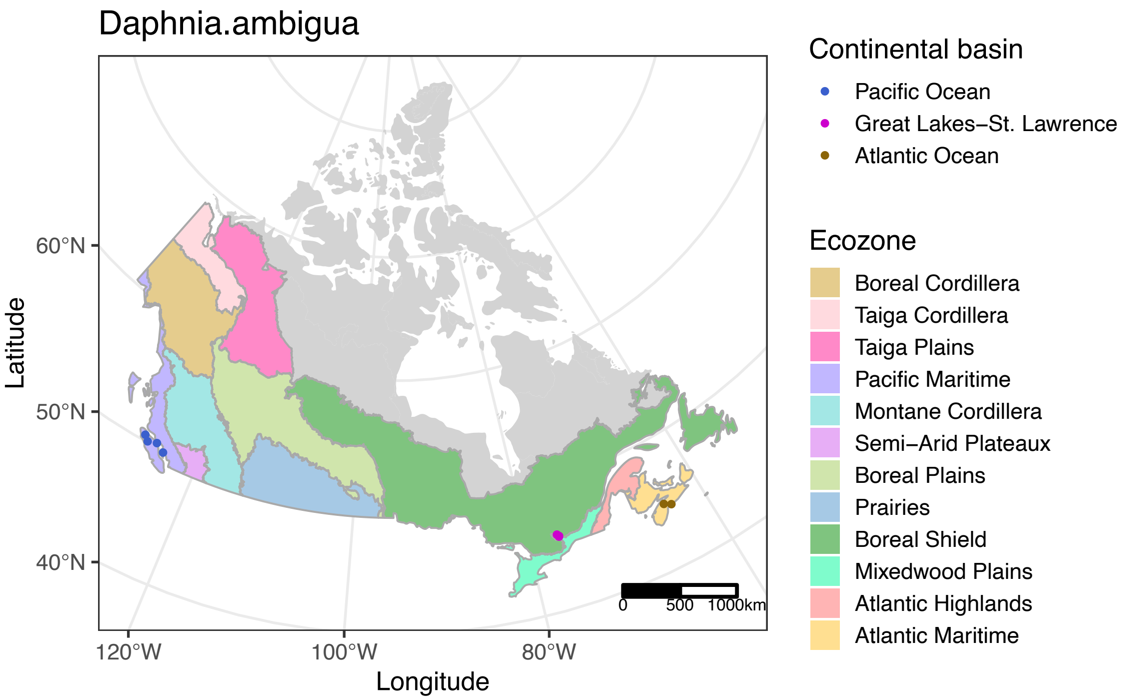
1000km


Daphnia.ambigua
Continental basin
Pacific Ocean
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
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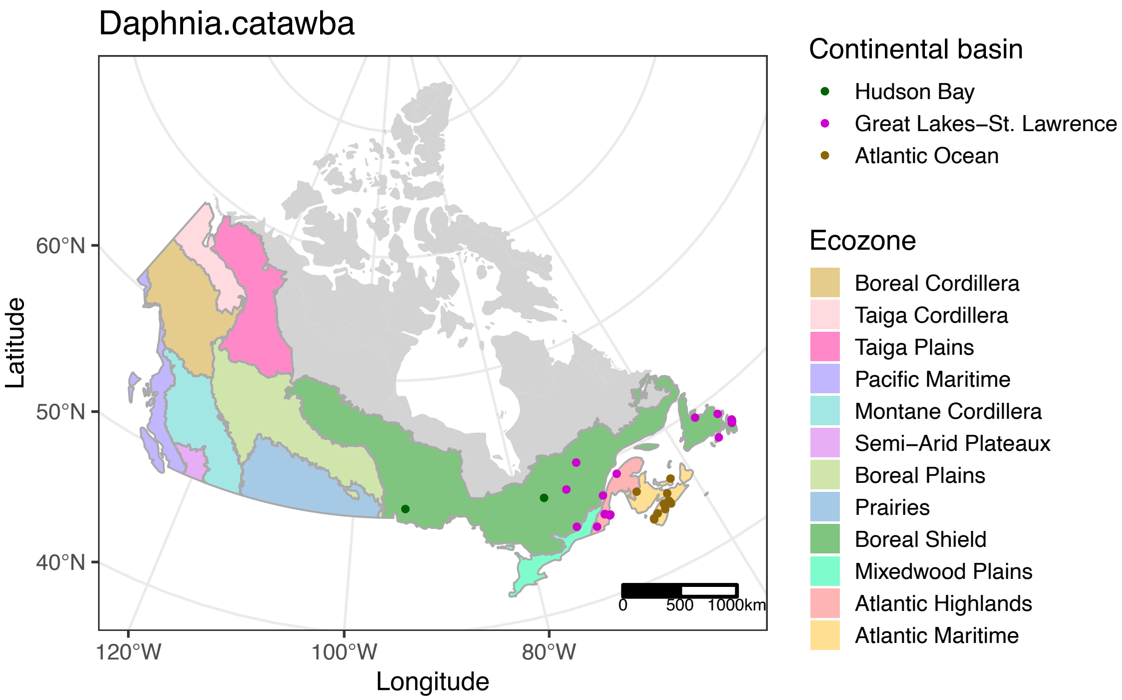
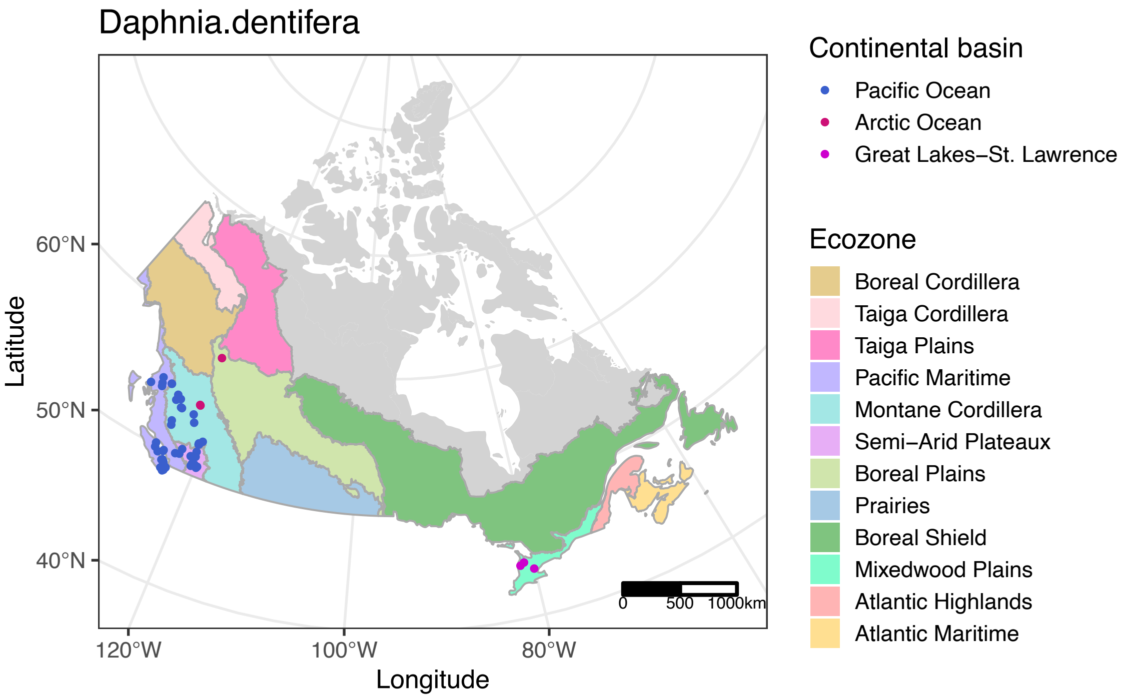
1000km


Daphnia.catawba
Continental basin
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
Latitude
60°N
50°N
40°N
120°W
100°W
80°W
Longitude
0
500
1000km


Daphnia.dentifera
Continental basin
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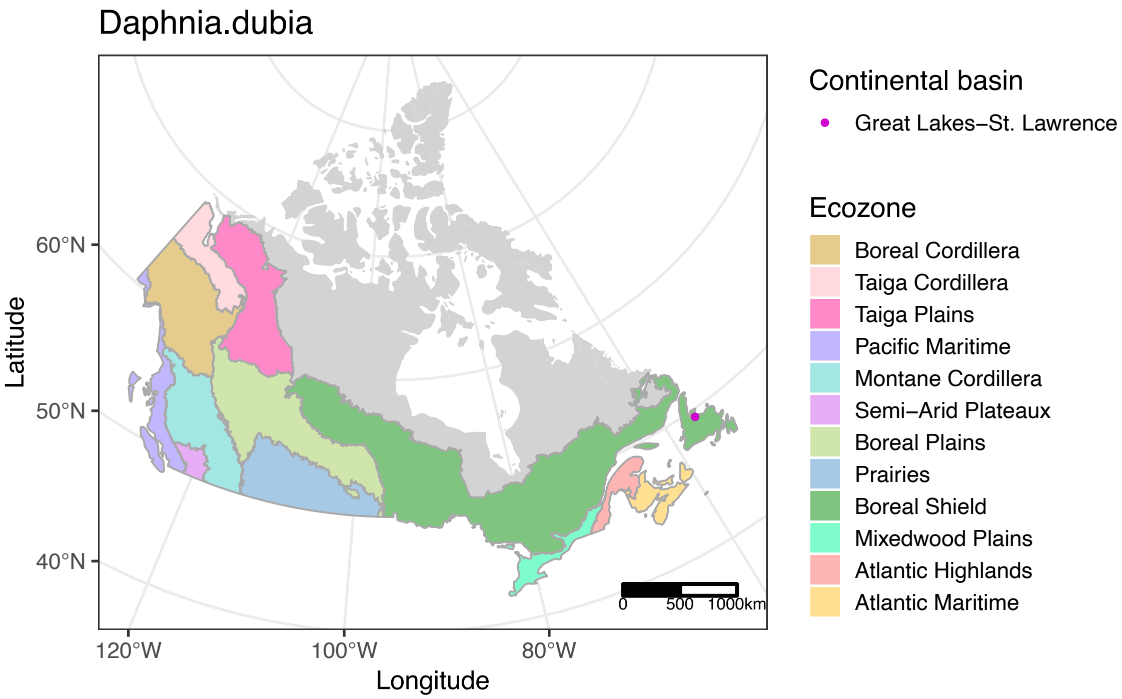
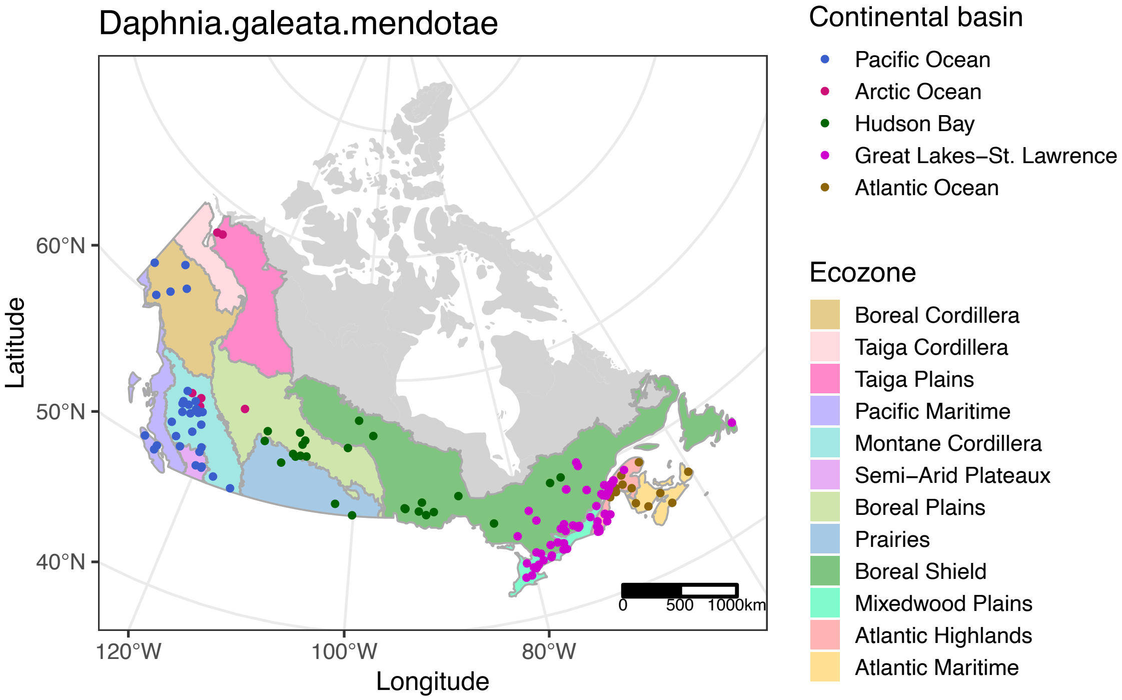
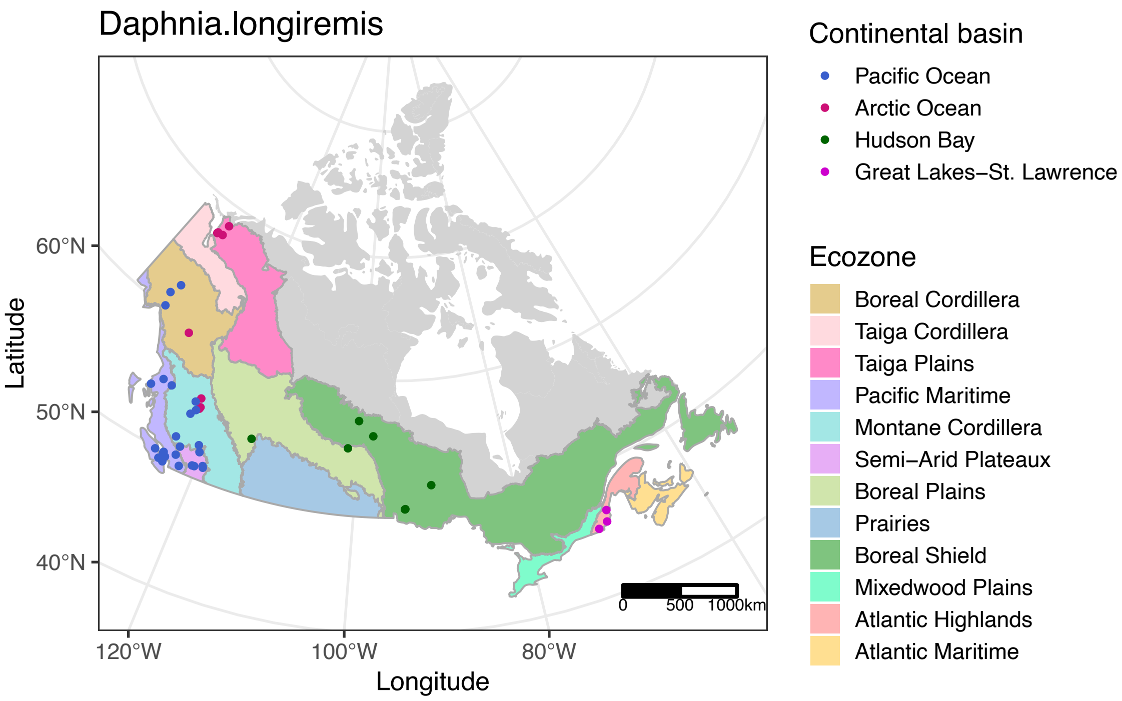
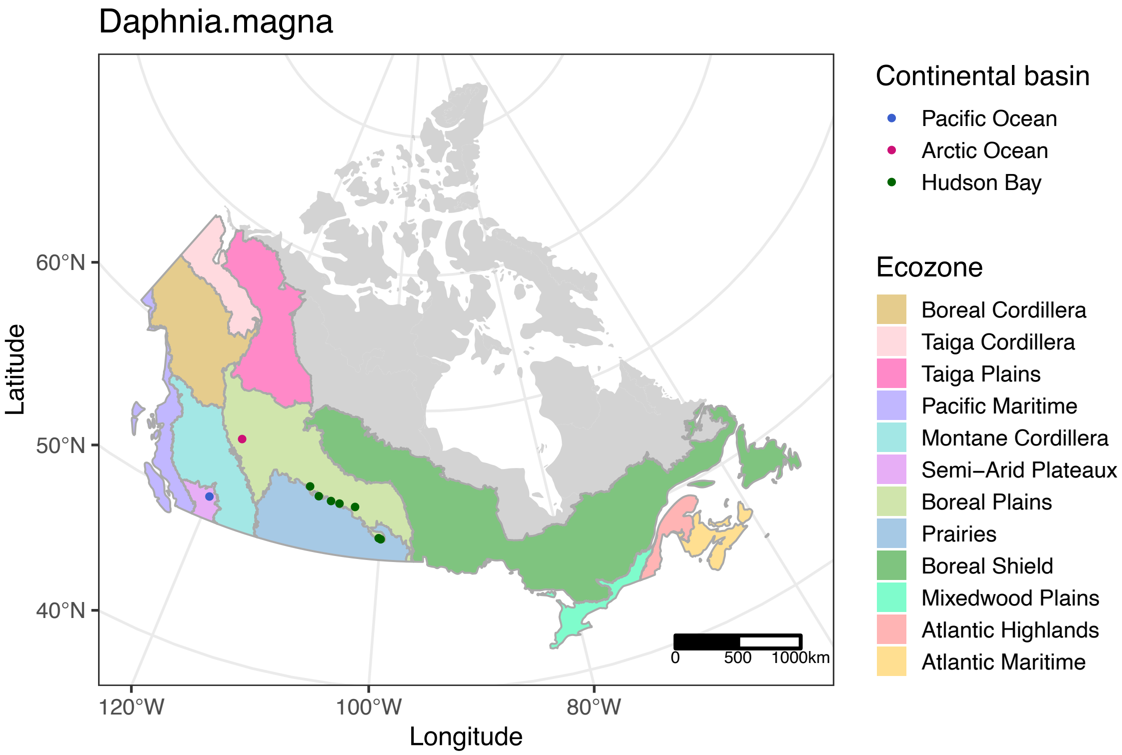
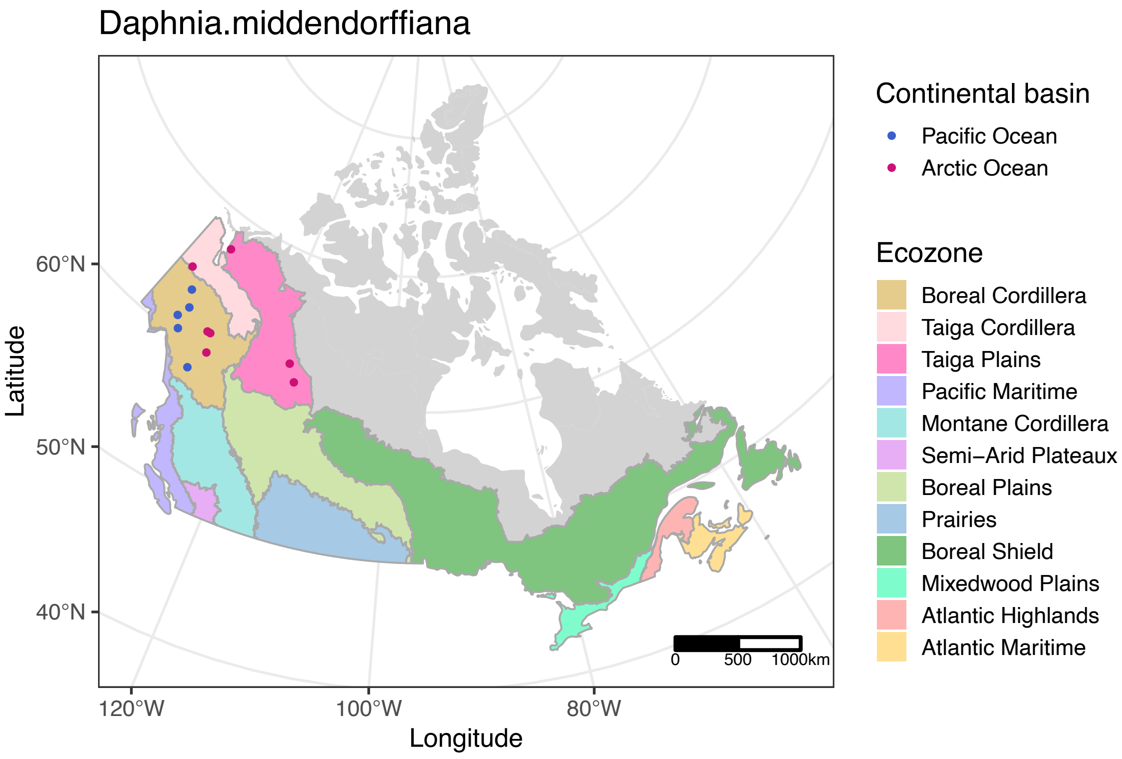
Arctic Ocean
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
Latitude
60°N
50°N
40°N
120°W
100°W
80°W
Longitude
0
500
1000km

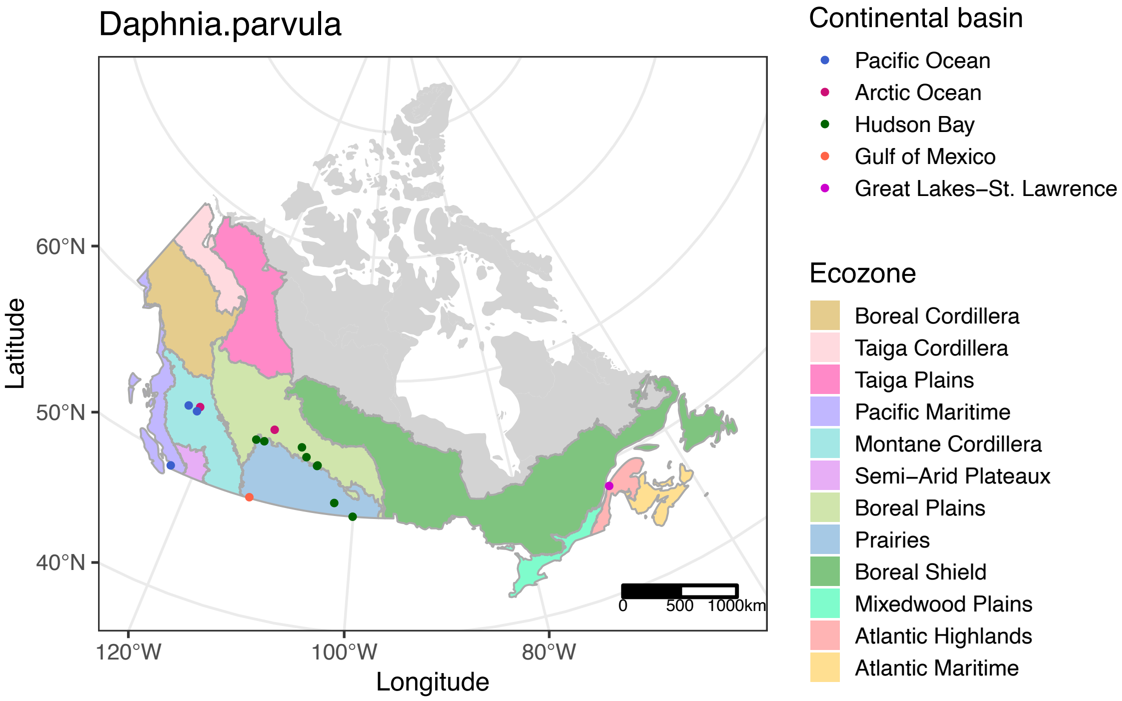

Daphnia.dubia
Continental basin
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km

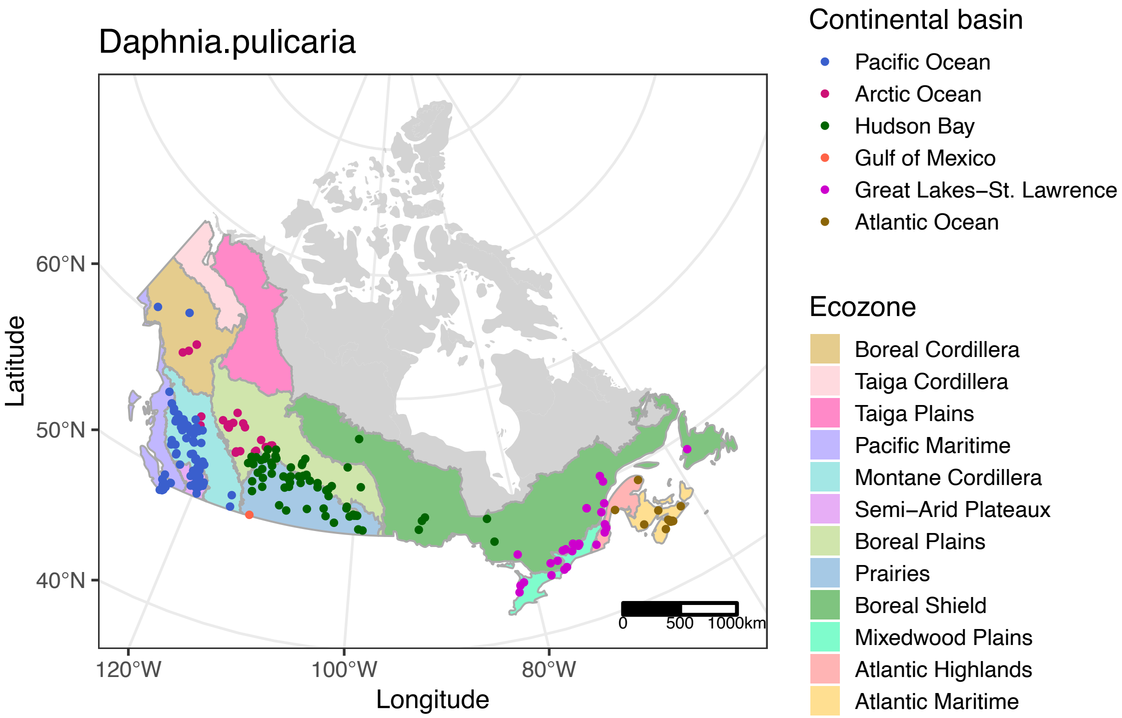

Daphnia.galeata.mendotae
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km


Daphnia.longiremis
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
● Pacific Ocean
● Arctic Ocean
● Hudson Bay
● Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Daphnia.magna
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
● Pacific Ocean
● Arctic Ocean
● Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Daphnia.middendorffiana


Daphnia.parvula


Daphnia.pulicaria
Latitude
60°N
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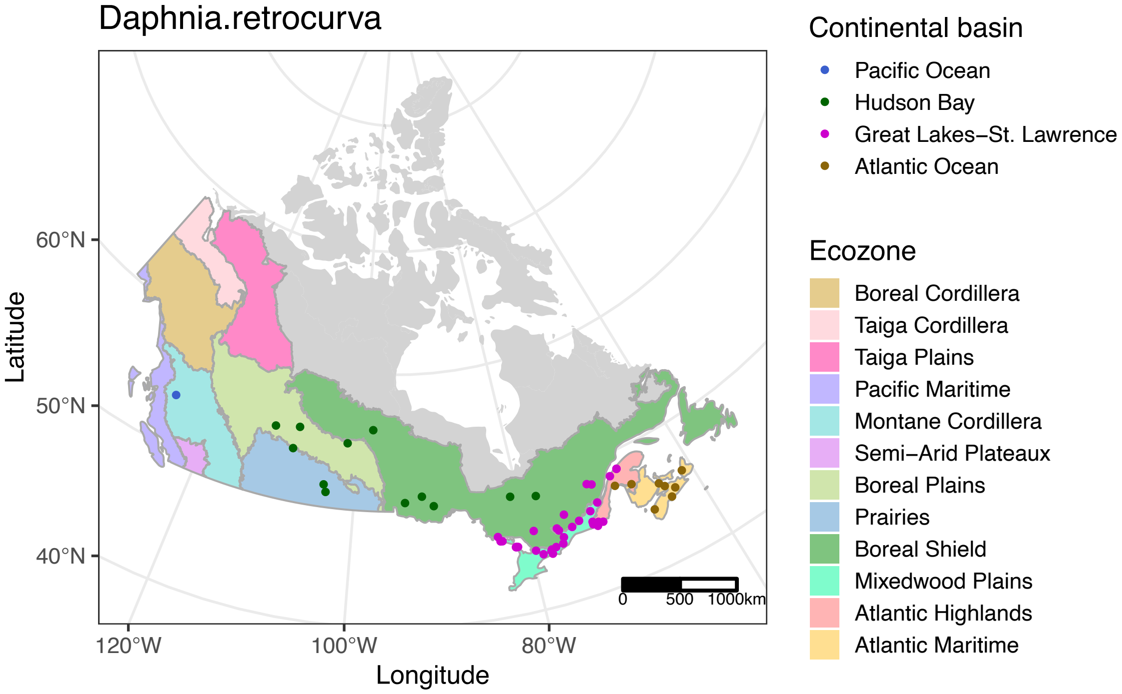
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Gulf of Mexico
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Daphnia.retrocurva
Latitude
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50°N
40°N
120°W
100°W
80°W
Longitude
0
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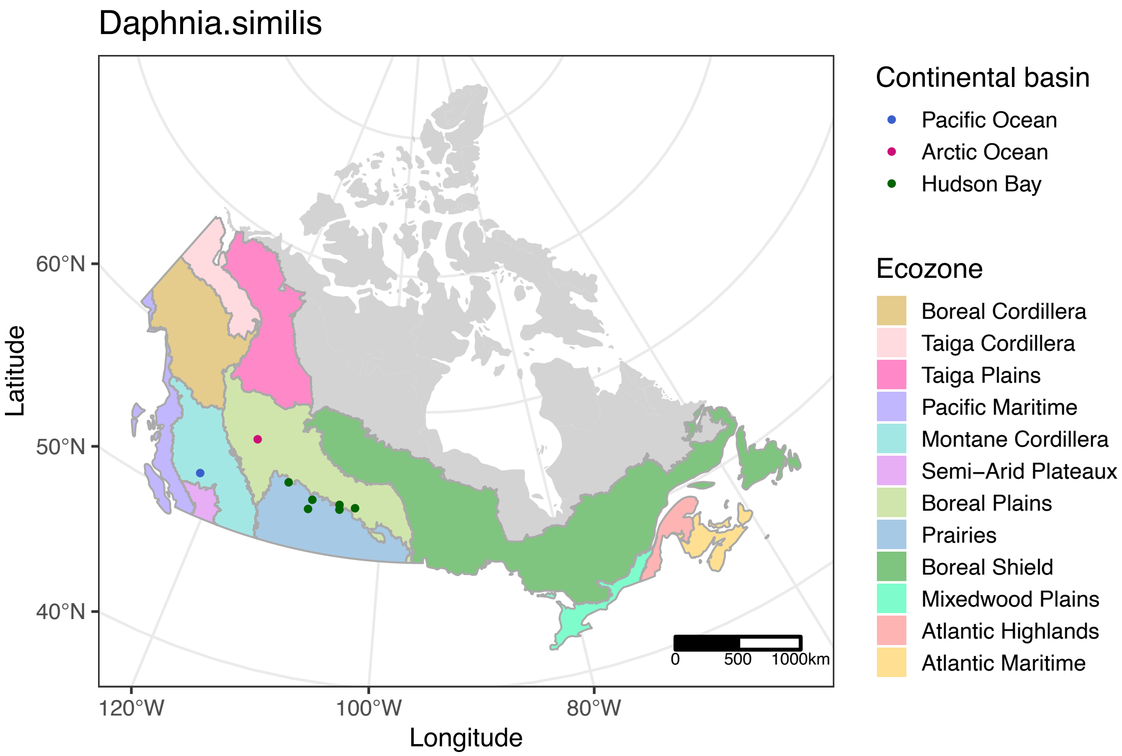
1000km
Continental basin
Pacific Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Daphnia.similis
Continental basin
● Pacific Ocean
● Arctic Ocean
● Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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Latitude
120°W
100°W
80°W
Longitude
0
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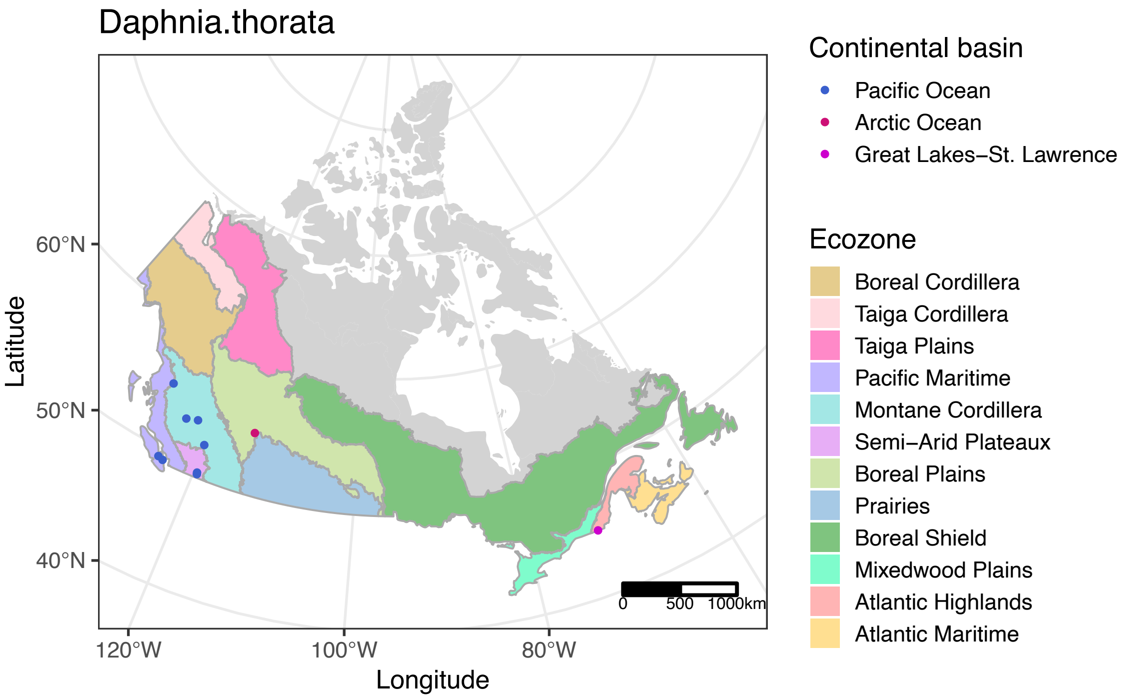
1000km


Daphnia.thorata
Continental basin
● Pacific Ocean
● Arctic Ocean
● Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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40°N
Latitude
120°W
100°W
80°W
Longitude
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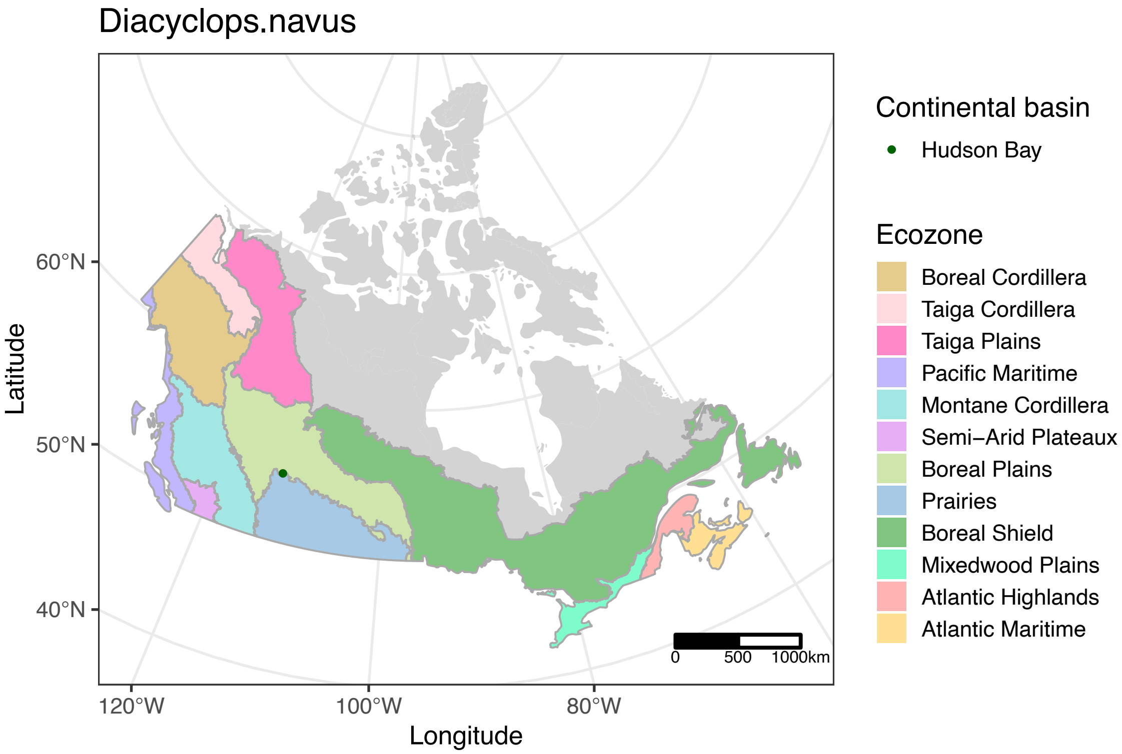
500
1000km


Diacyclops.navus
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Latitude
120°W
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80°W
Longitude
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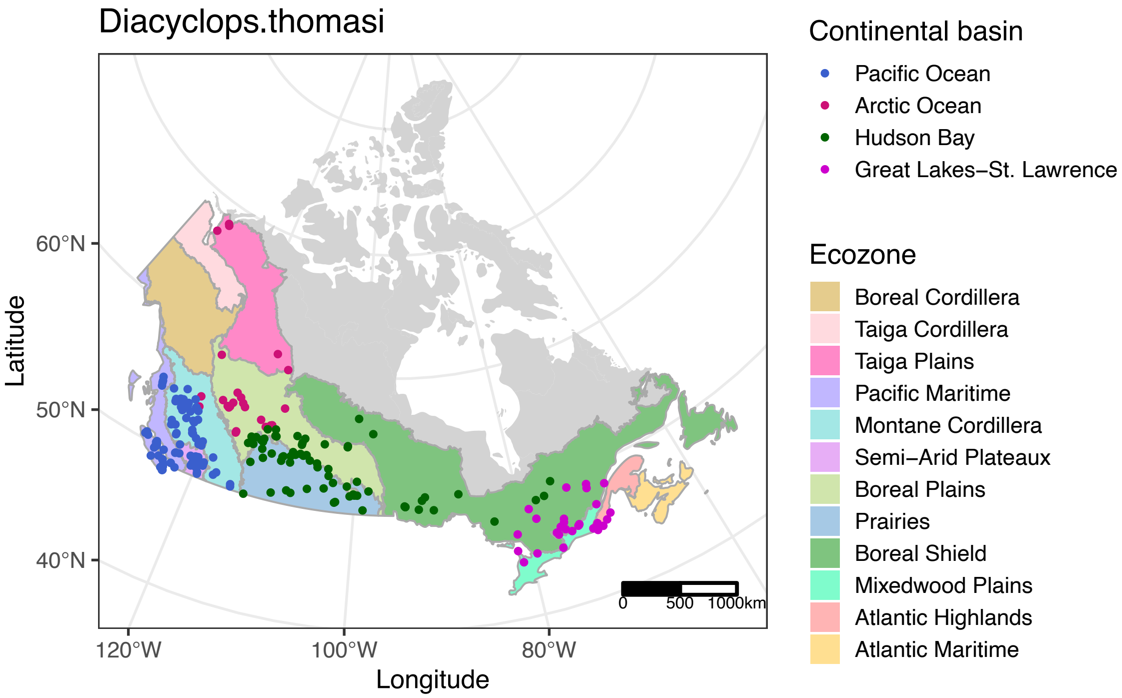
1000km
Continental basin
Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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Latitude
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Longitude
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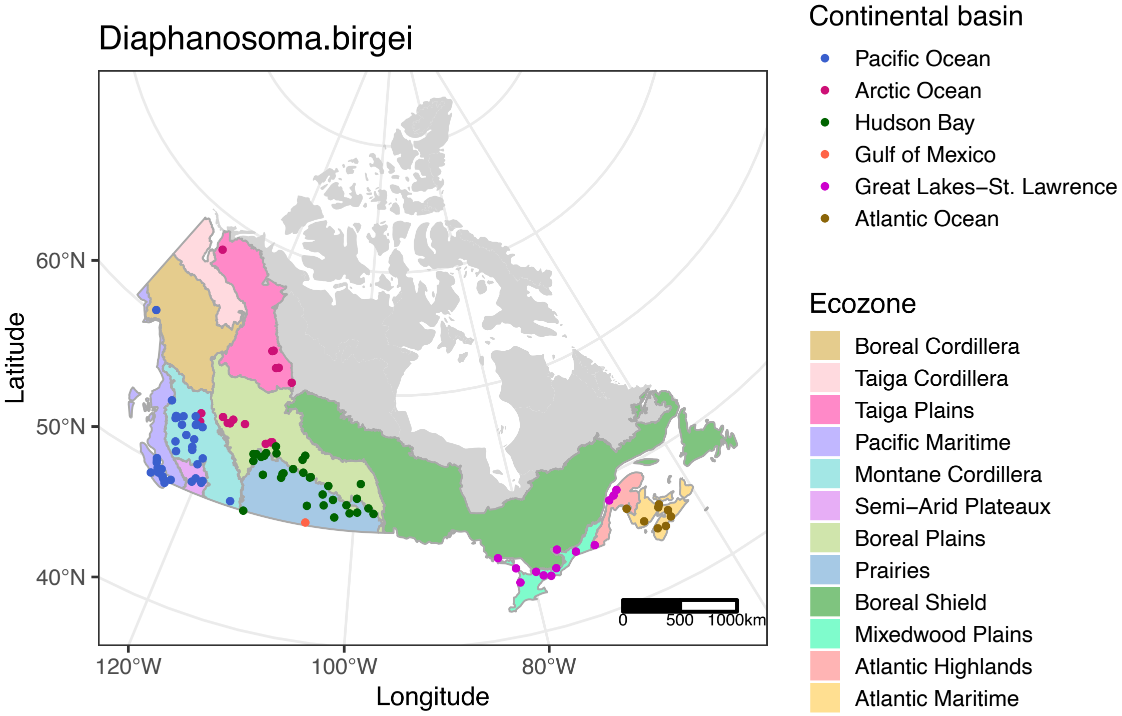
1000km
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Diaphanosoma.birgei
60°N
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Latitude
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100°W
80°W
Longitude
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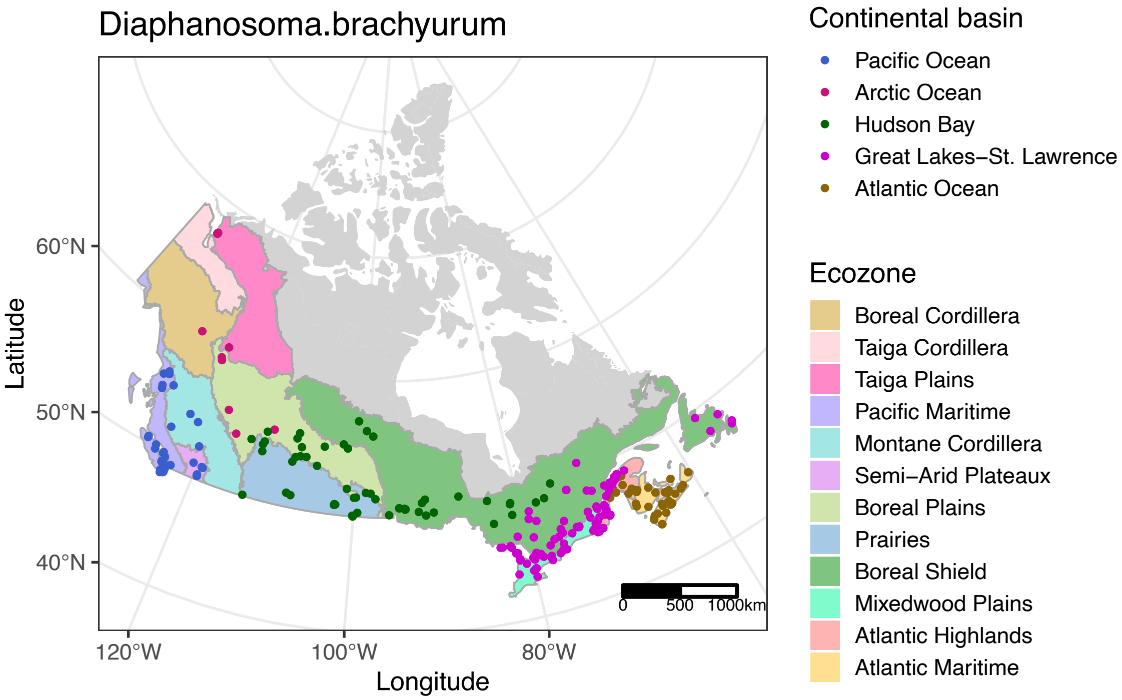
1000km
Continental basin
● Pacific Ocean
● Arctic Ocean
● Hudson Bay
● Gulf of Mexico
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Diaphanosoma.brachyurum
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100°W
80°W
Longitude
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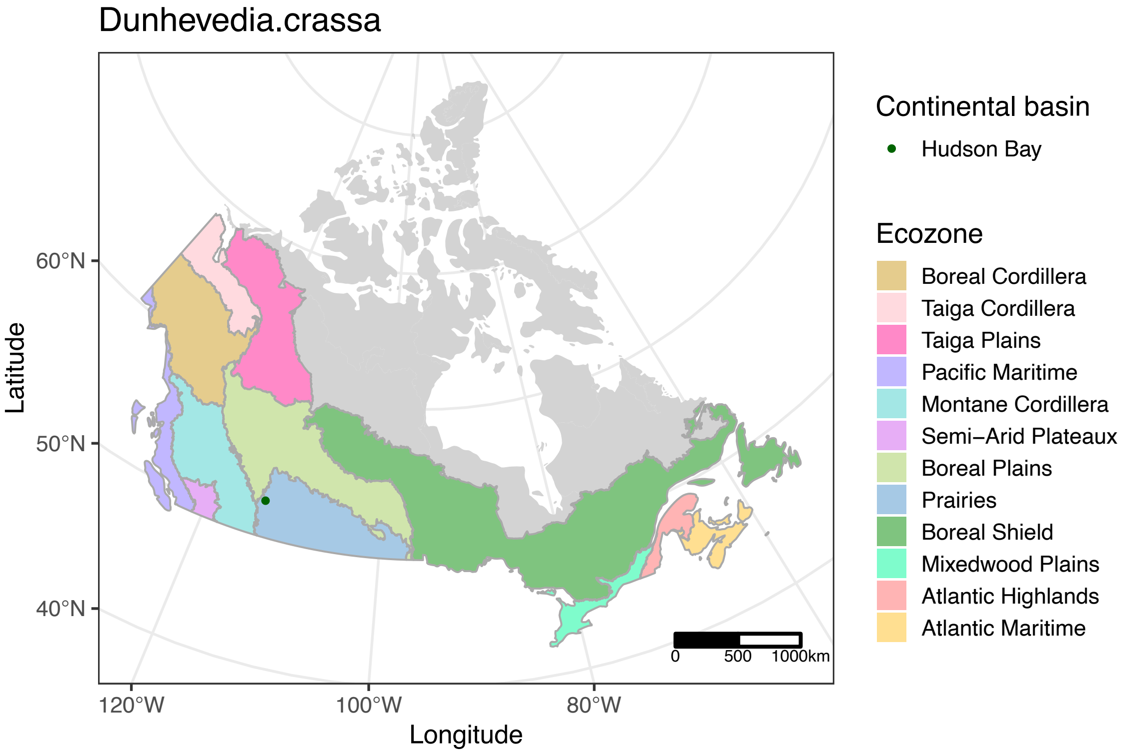
1000km
Continental basin
● Pacific Ocean
● Arctic Ocean
● Hudson Bay
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Dunhevedia.crassa
Continental basin
Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
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Latitude
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100°W
80°W
Longitude
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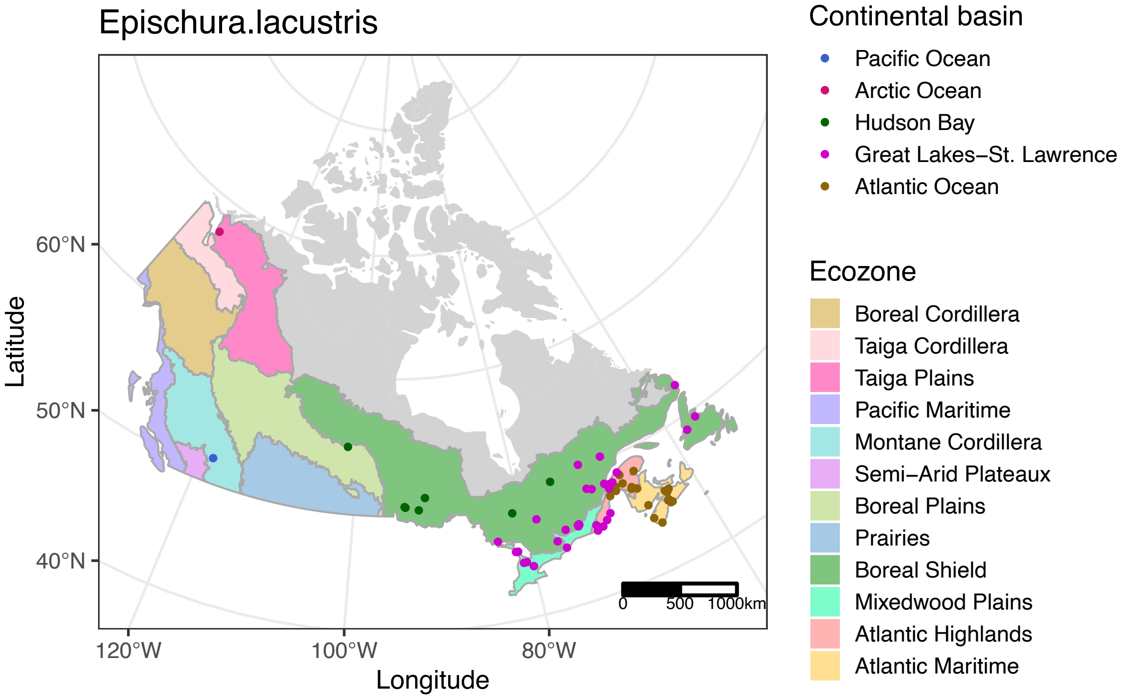
500
1000km


Epischura.lacustris
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
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100°W
80°W
Longitude
0
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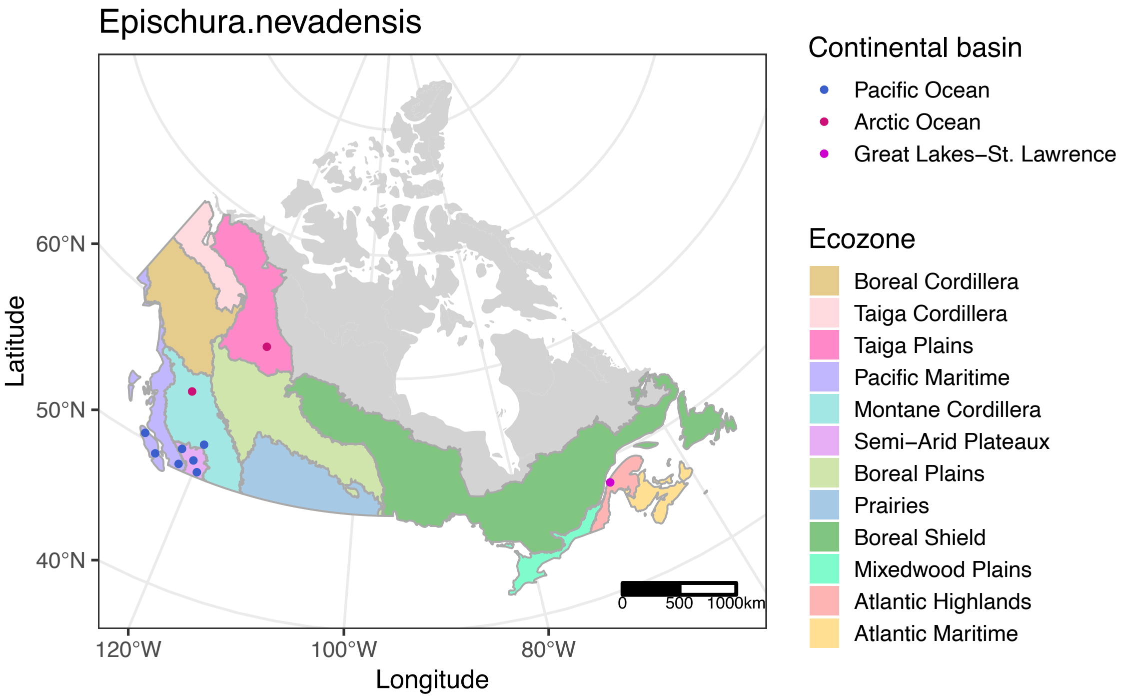
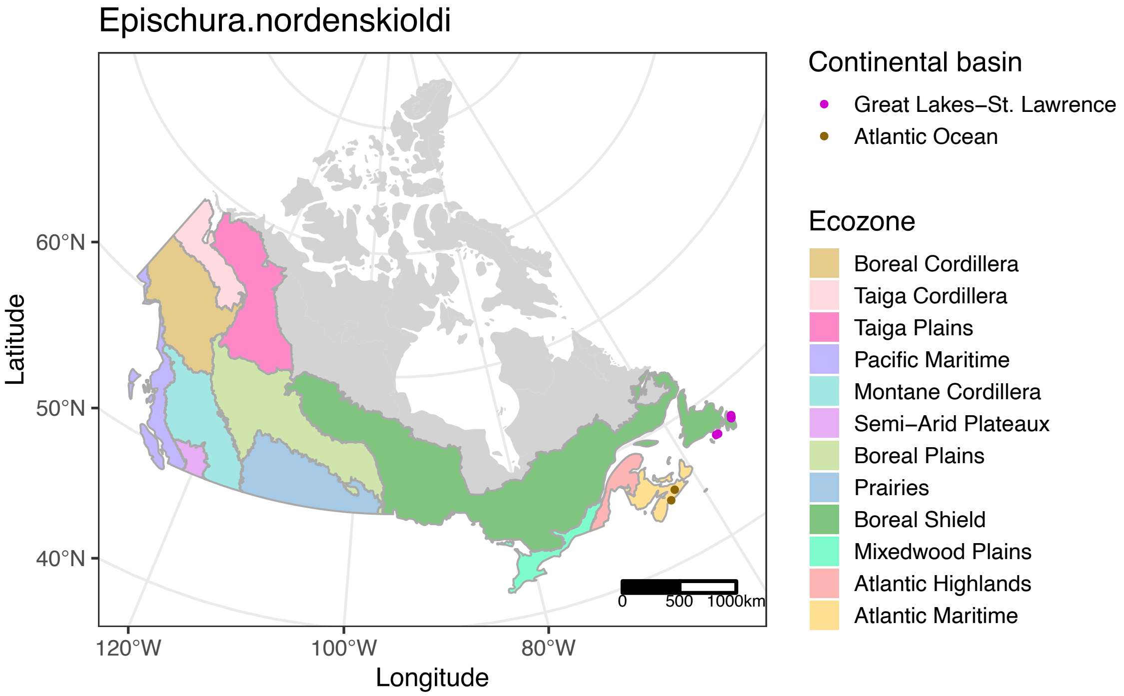
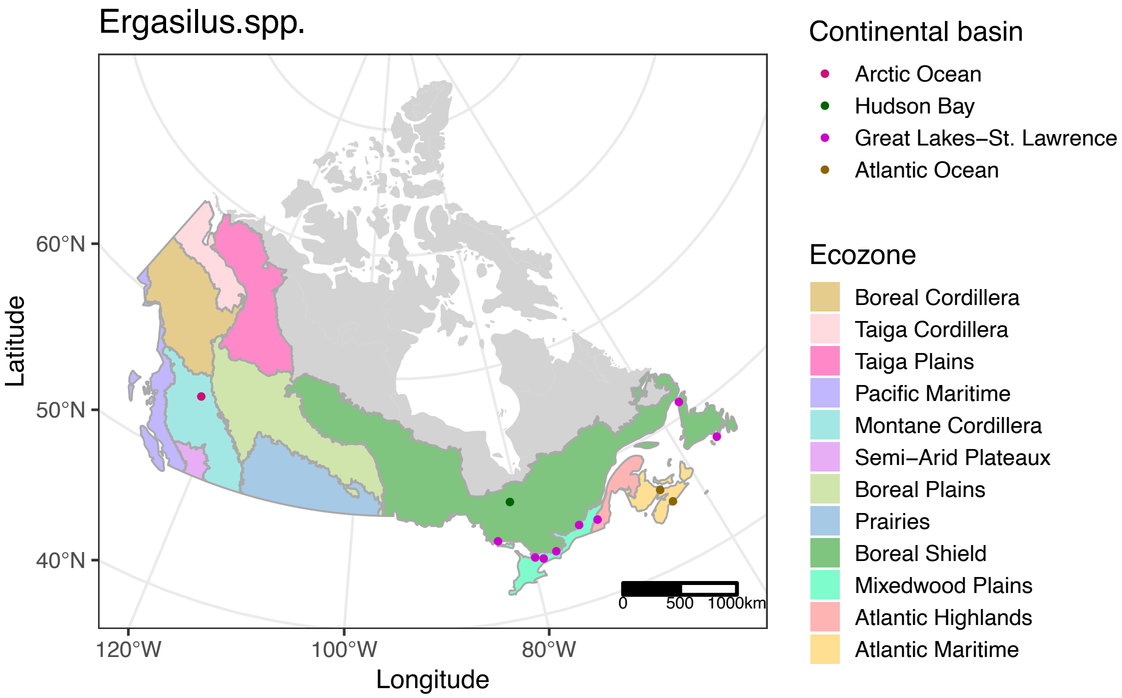
1000km


Epischura.nevadensis


Epischura.nordenskioldi


Ergasilus.spp.
60°N
50°N
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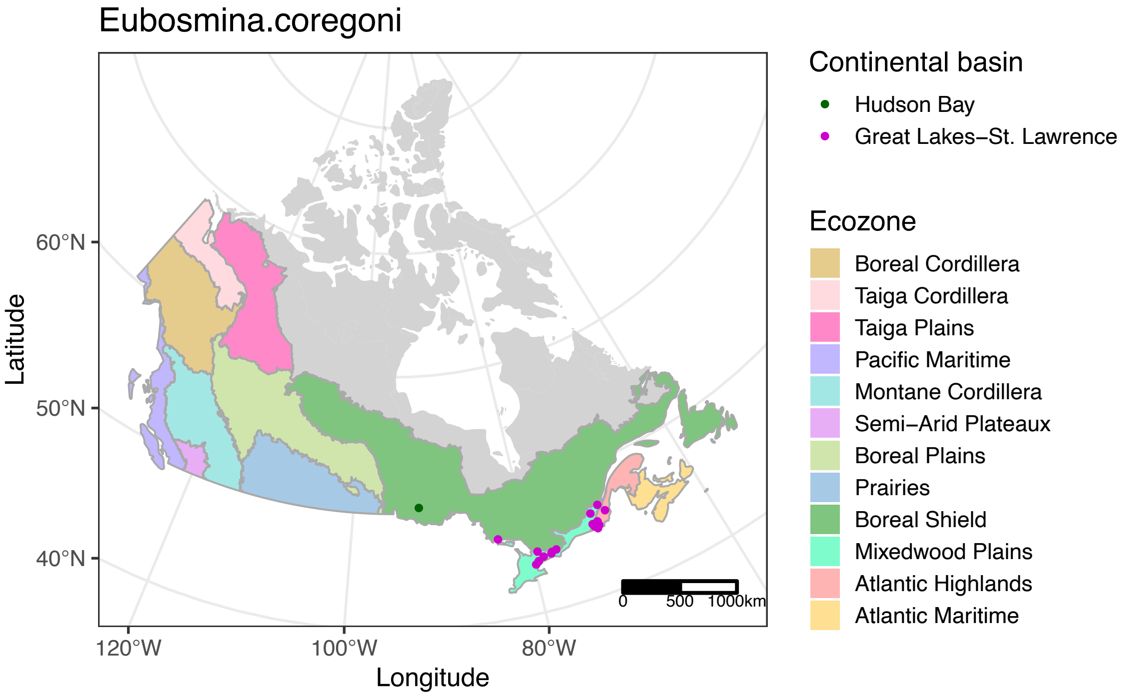
Latitude
120°W
100°W
80°W
Longitude
0 500 1000km
Continental basin
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Eubosmina.coregoni
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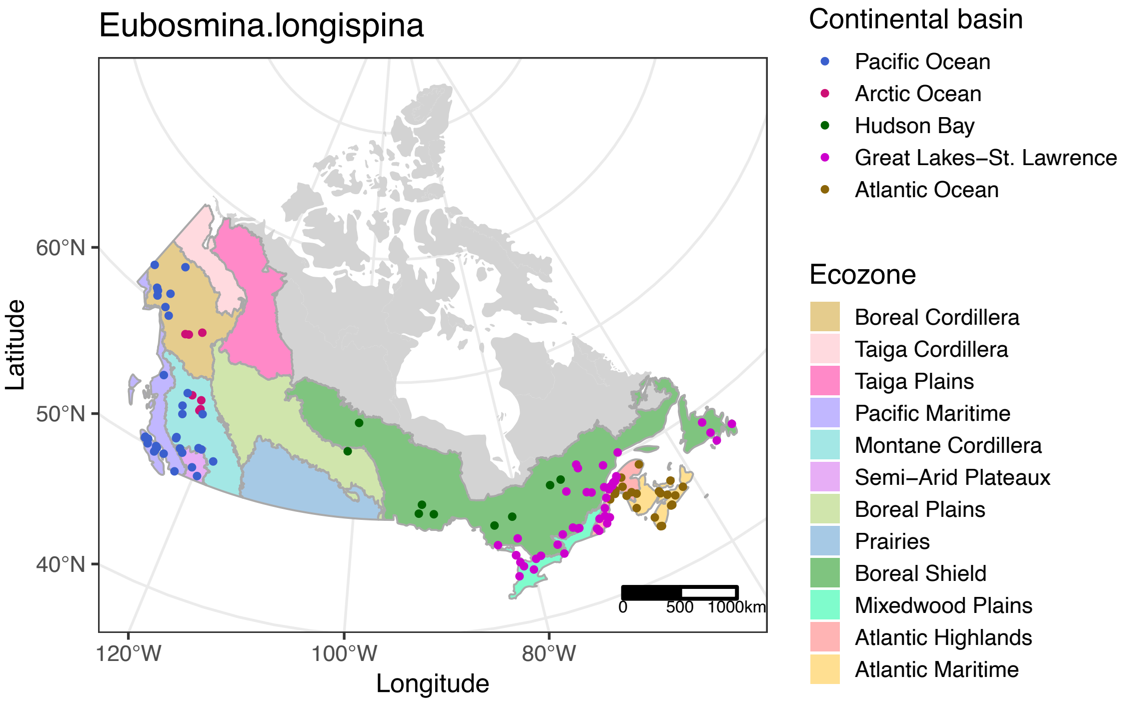
40°N
Latitude
120°W
100°W
80°W
Longitude
0 500 1000km
Continental basin
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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Latitude
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Longitude
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1000km
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
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Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
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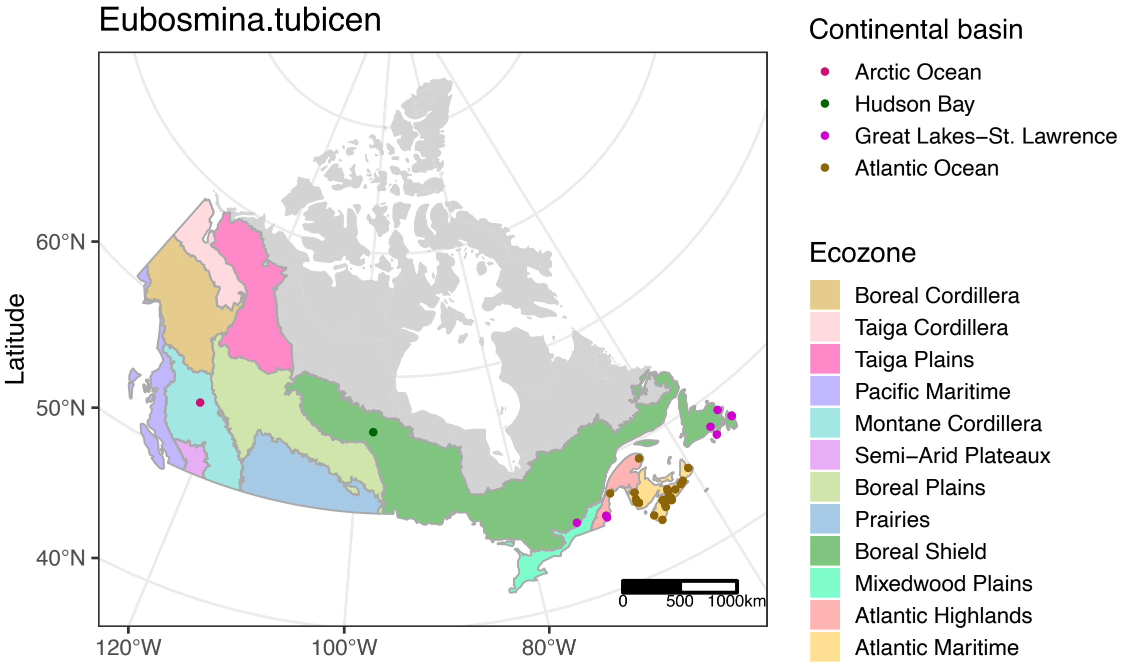
Atlantic Highlands
Atlantic Maritime


Eubosmina.tubicen
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Latitude
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Longitude
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1000km
Continental basin
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
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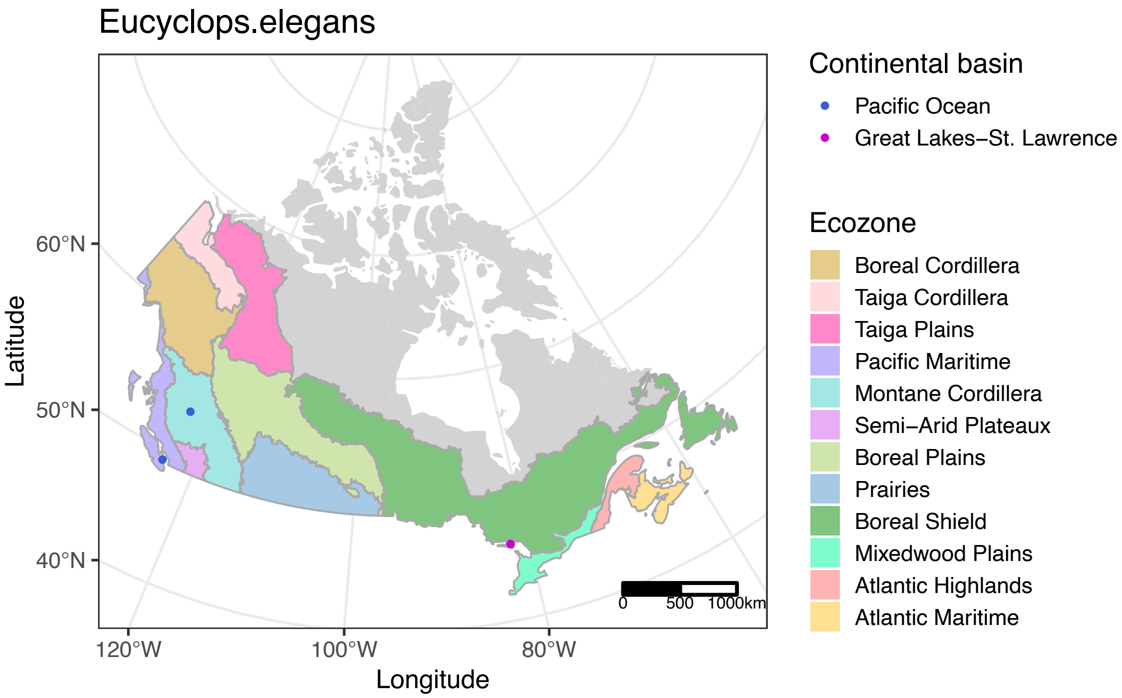
Atlantic Highlands
Atlantic Maritime


Eucyclops.elegans
Continental basin
Pacific Ocean
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
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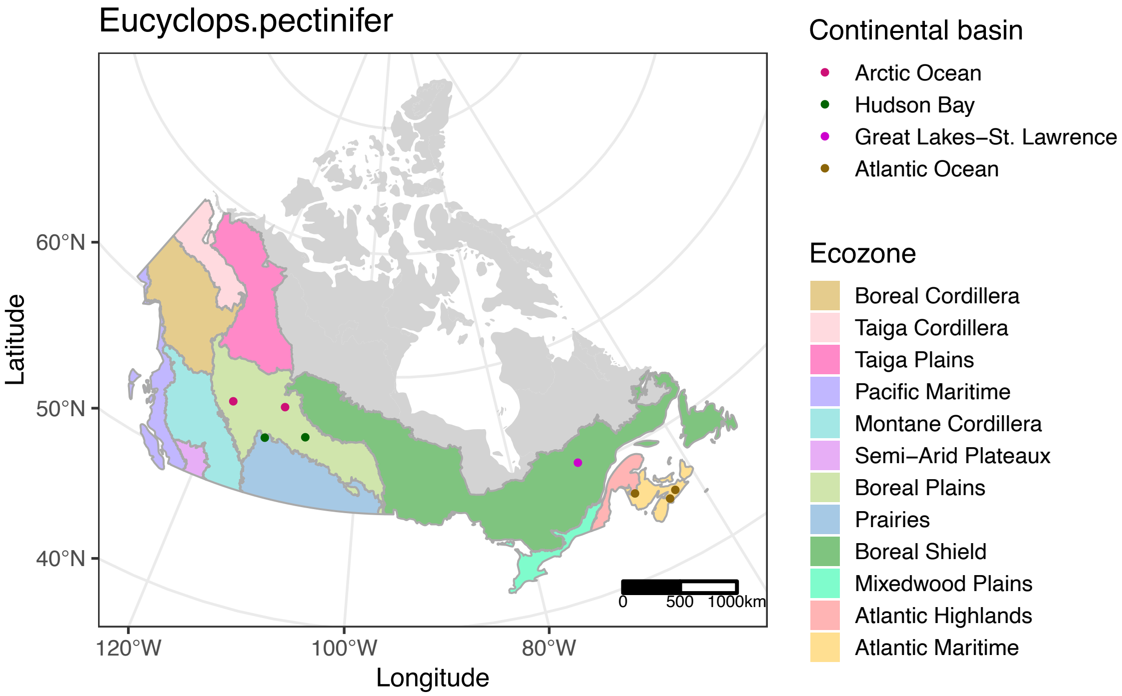
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km


Eucyclops.pectinifer
Continental basin
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
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100°W
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Longitude
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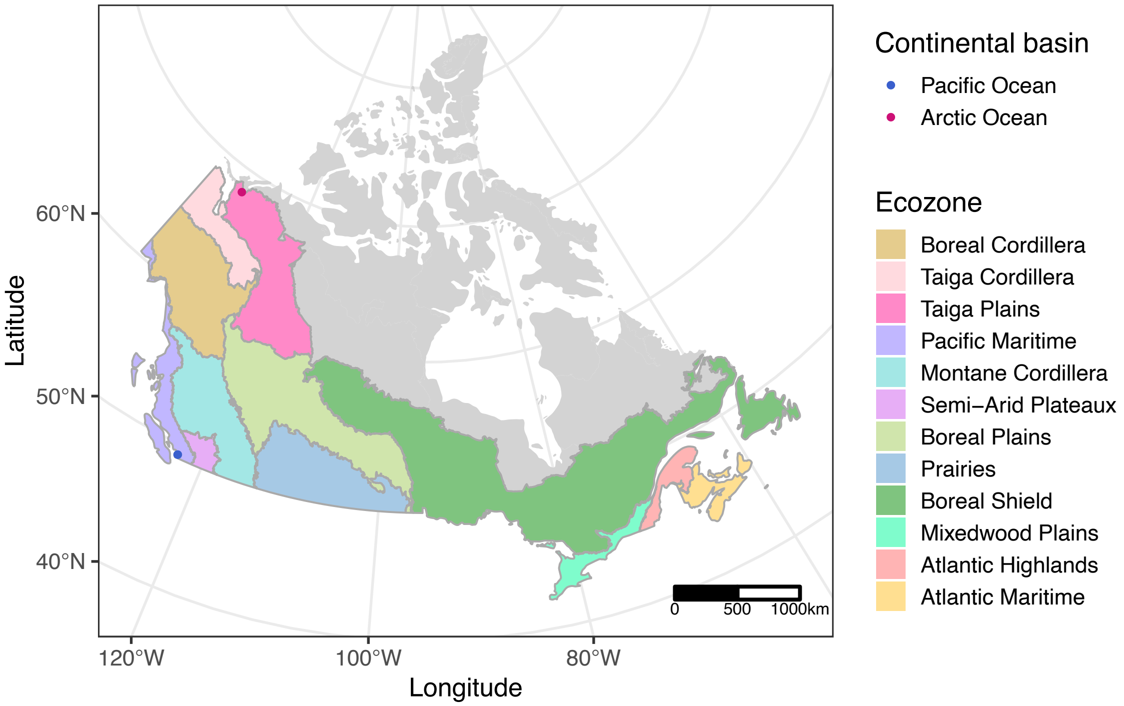
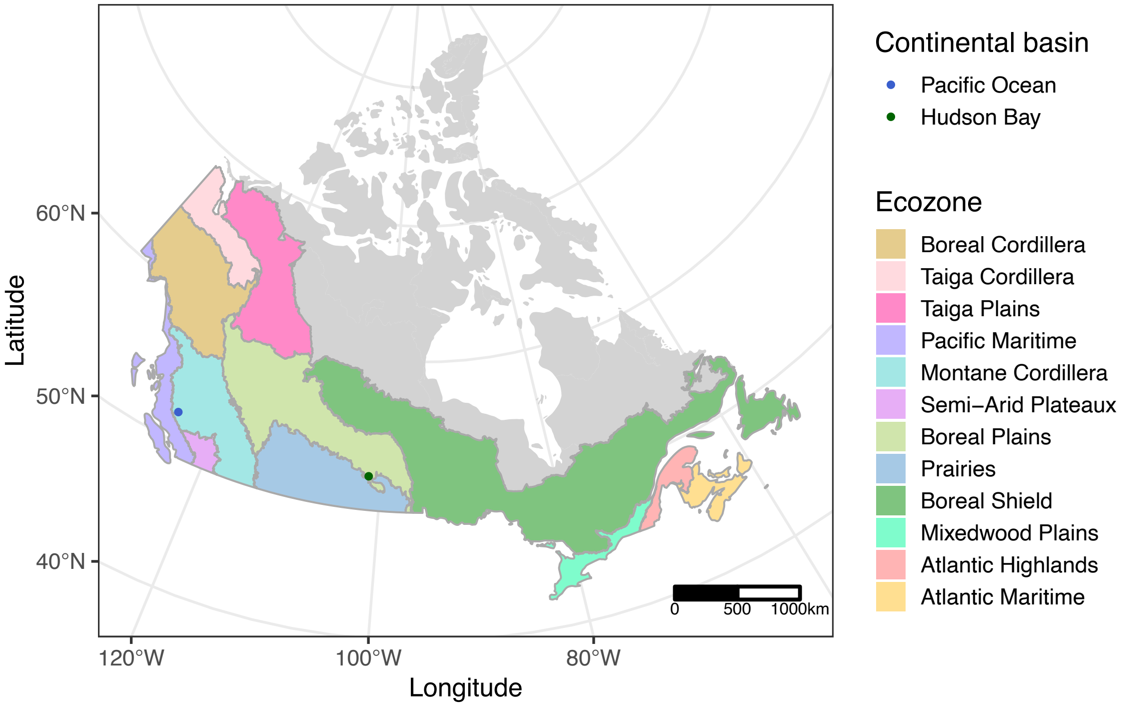
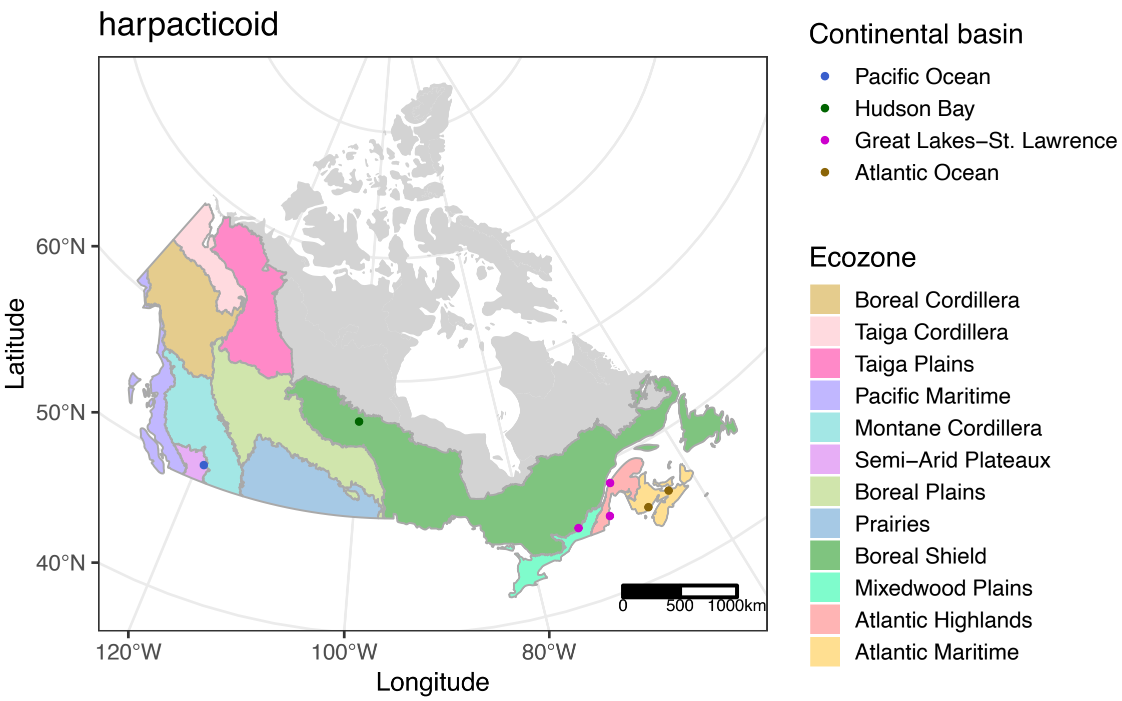
1000km

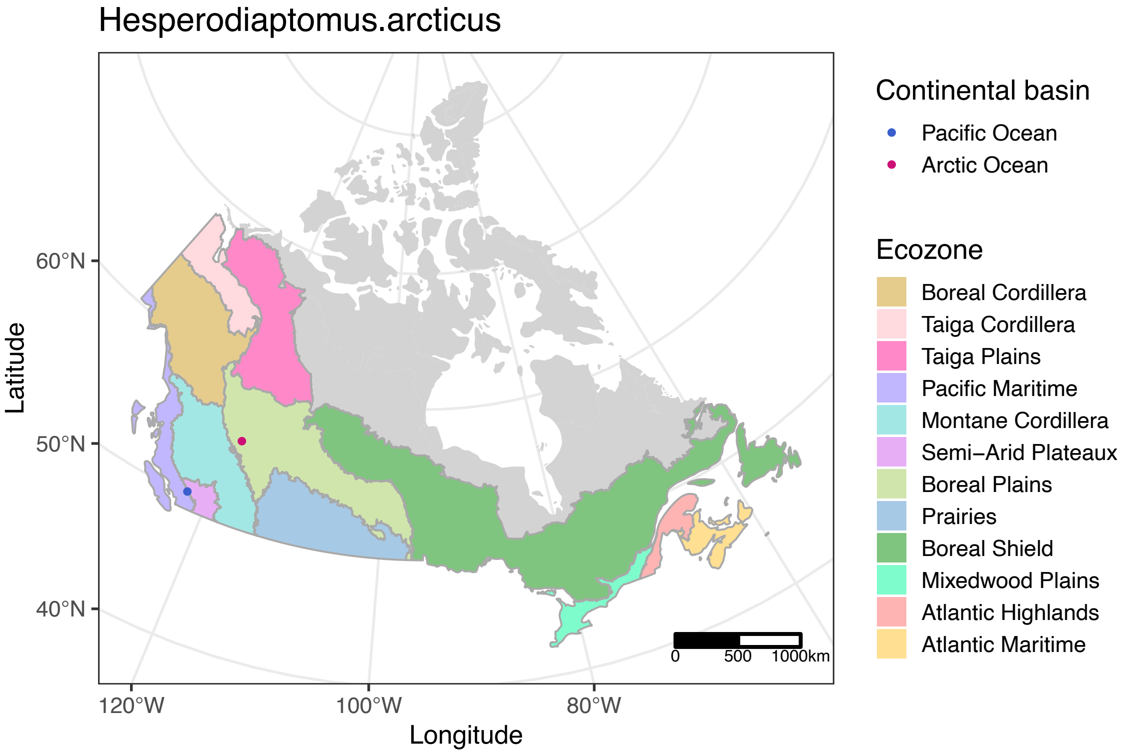


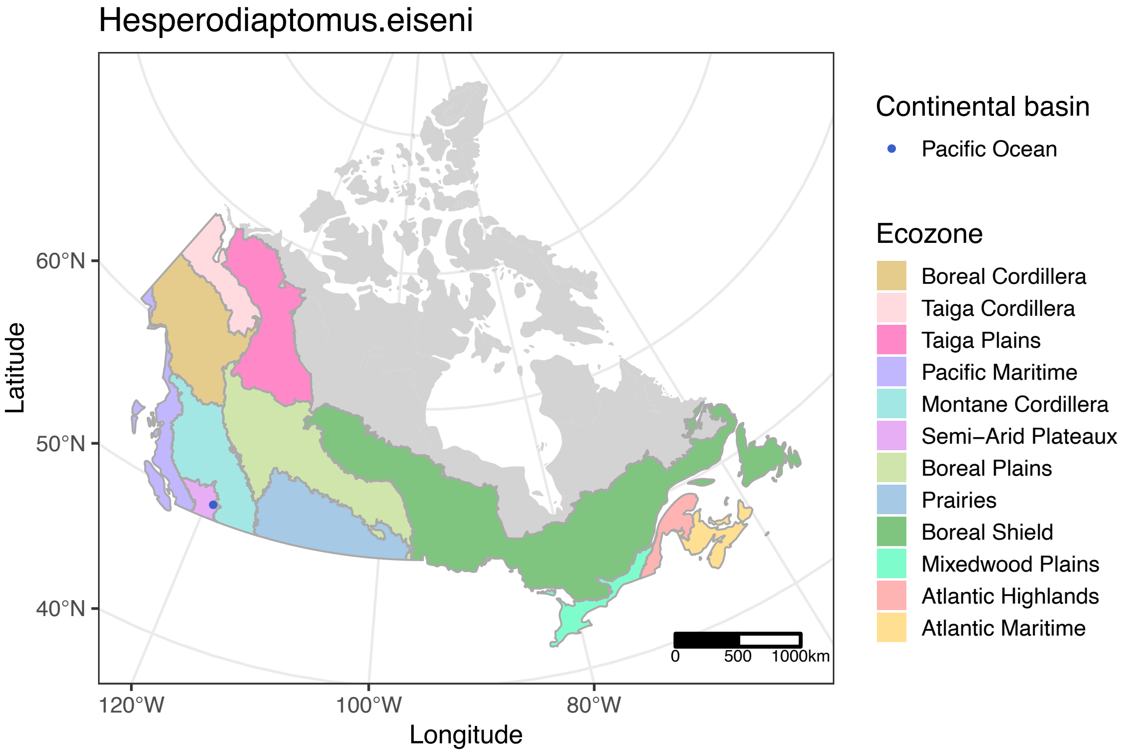
Eurycercus.spp.



Graptoleberis.testudinaria


harpacticoid


Hesperodiaptomus.arcticus



Hesperodiaptomus.eiseni
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
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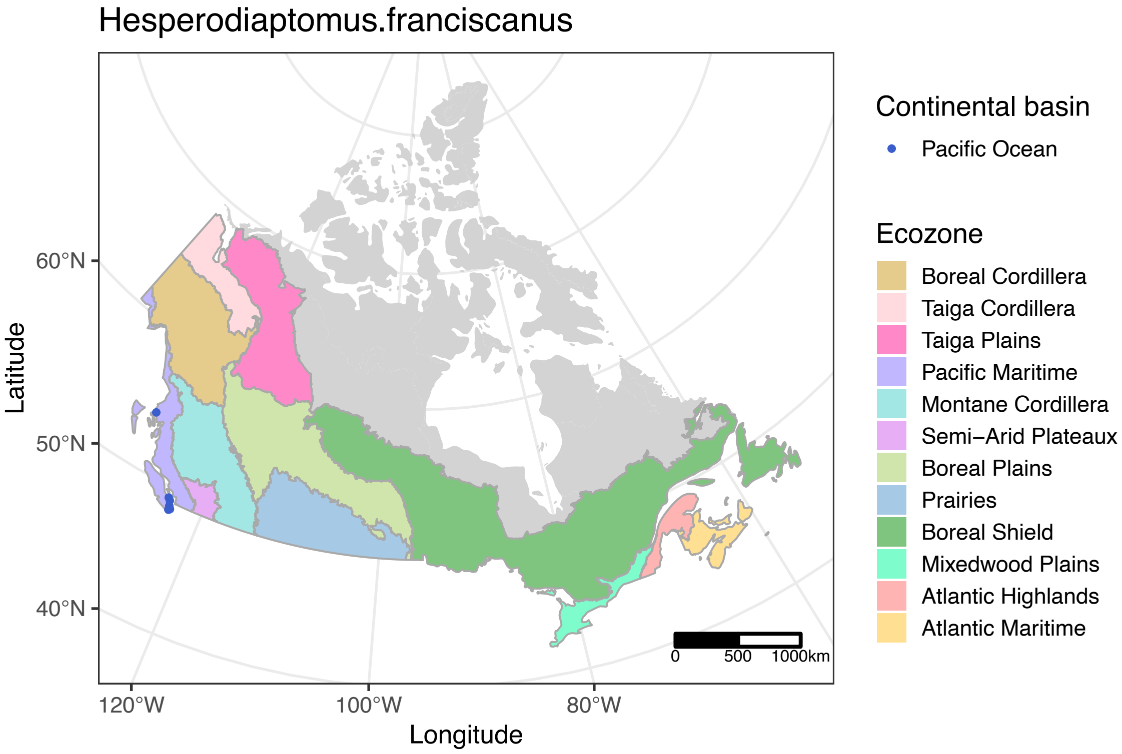
500
1000km
Continental basin
Pacific Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime



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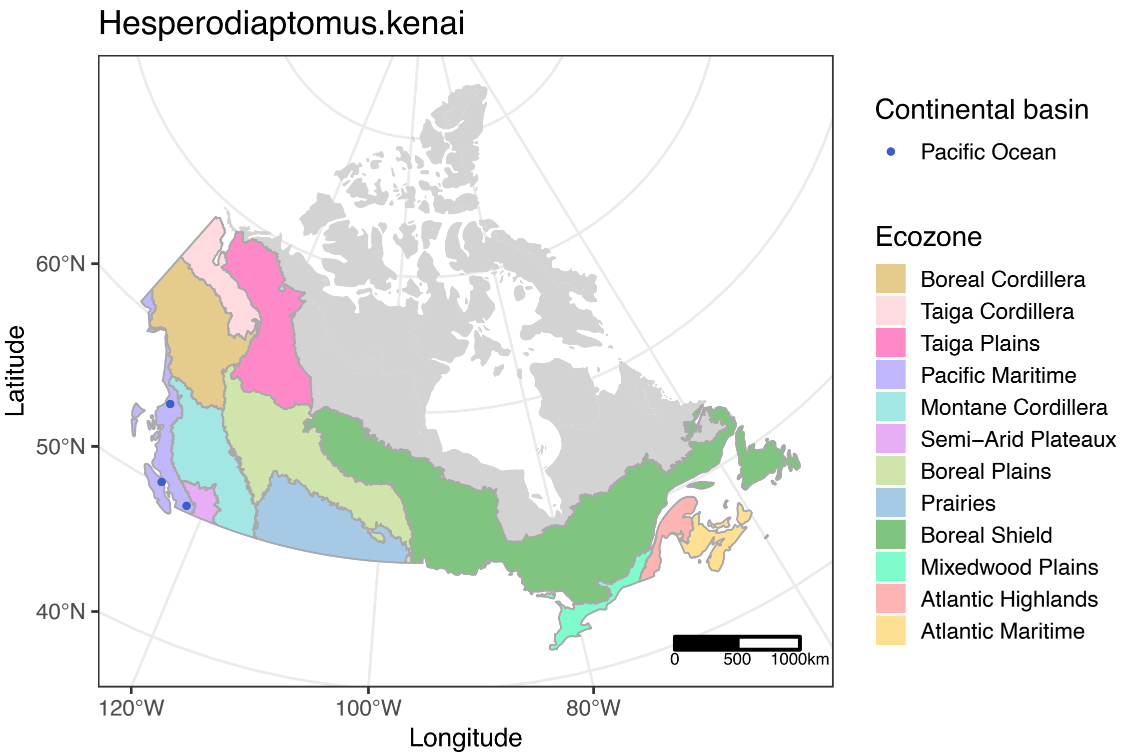
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
Pacific Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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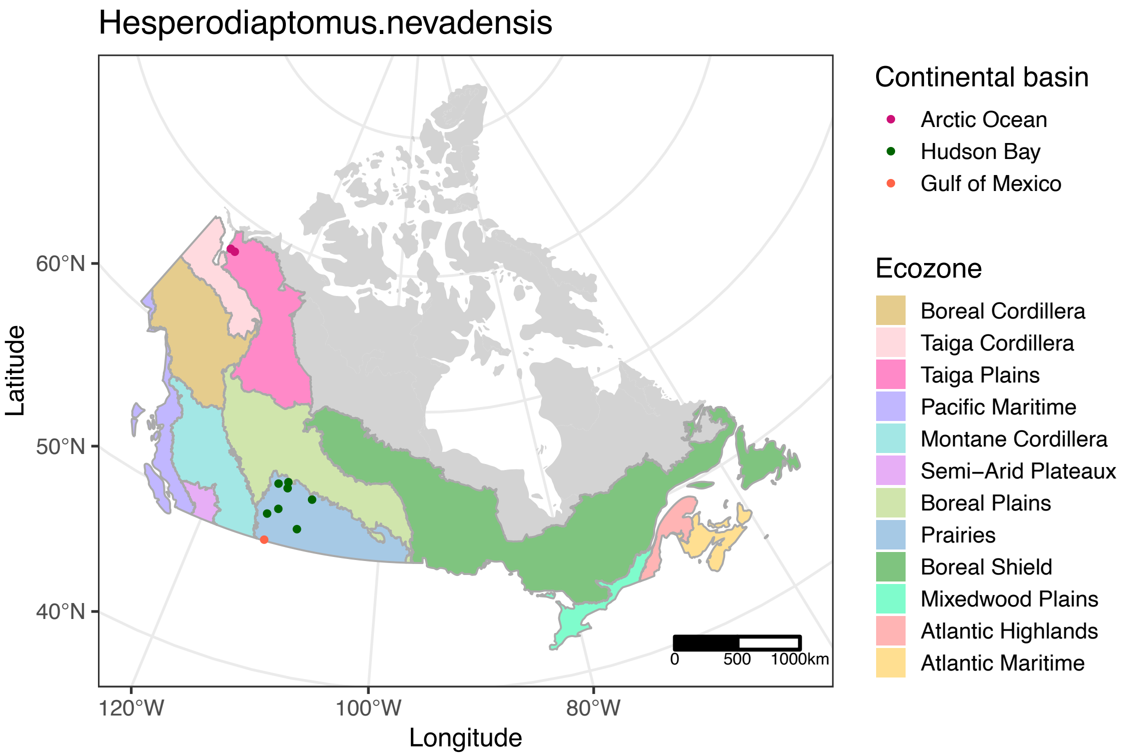
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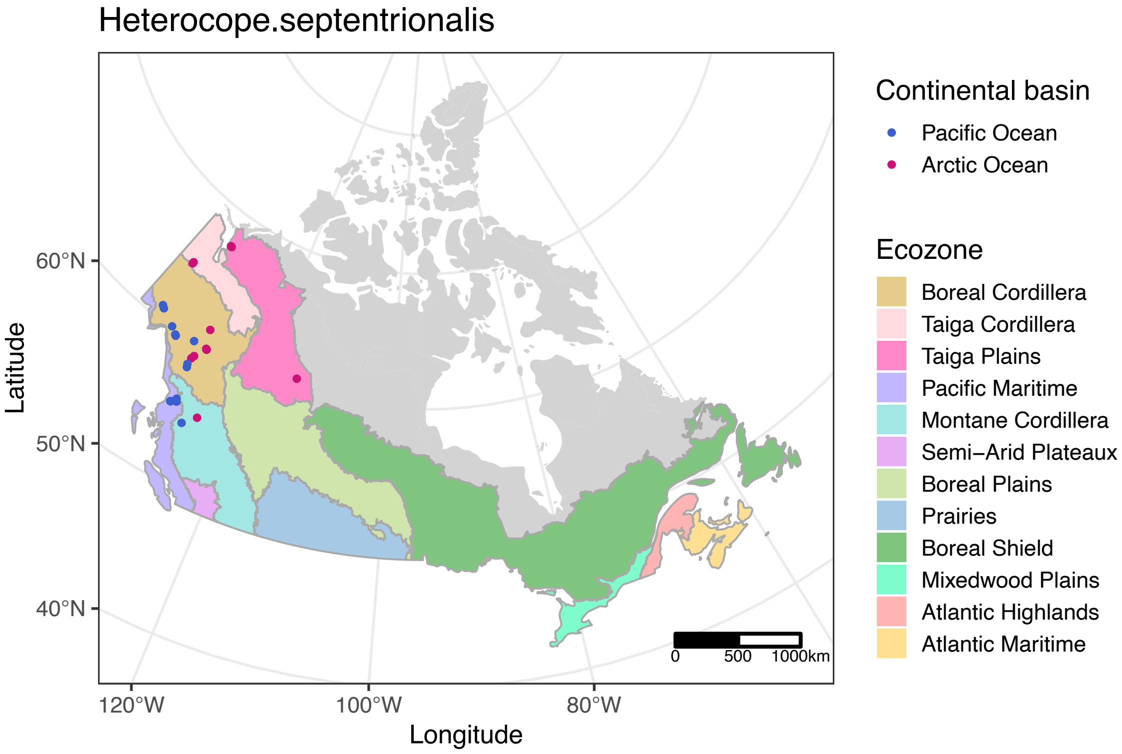
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Continental basin
Pacific Ocean
Arctic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
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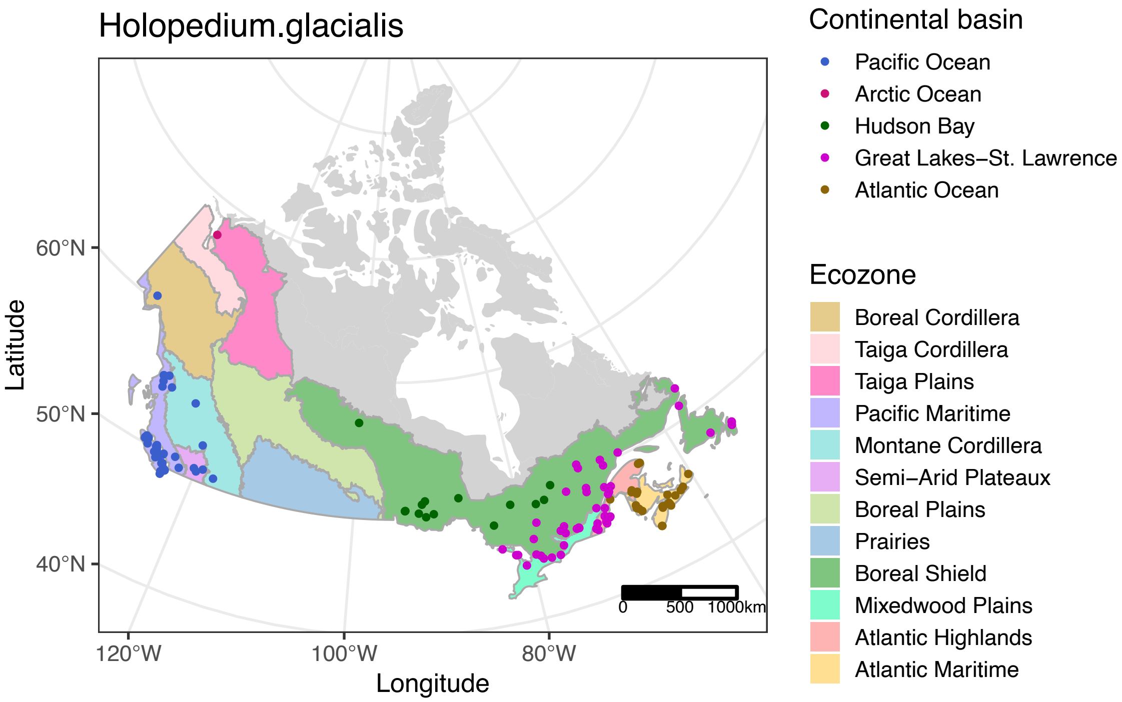
100°W
80°W
Longitude
0
500
1000km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Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
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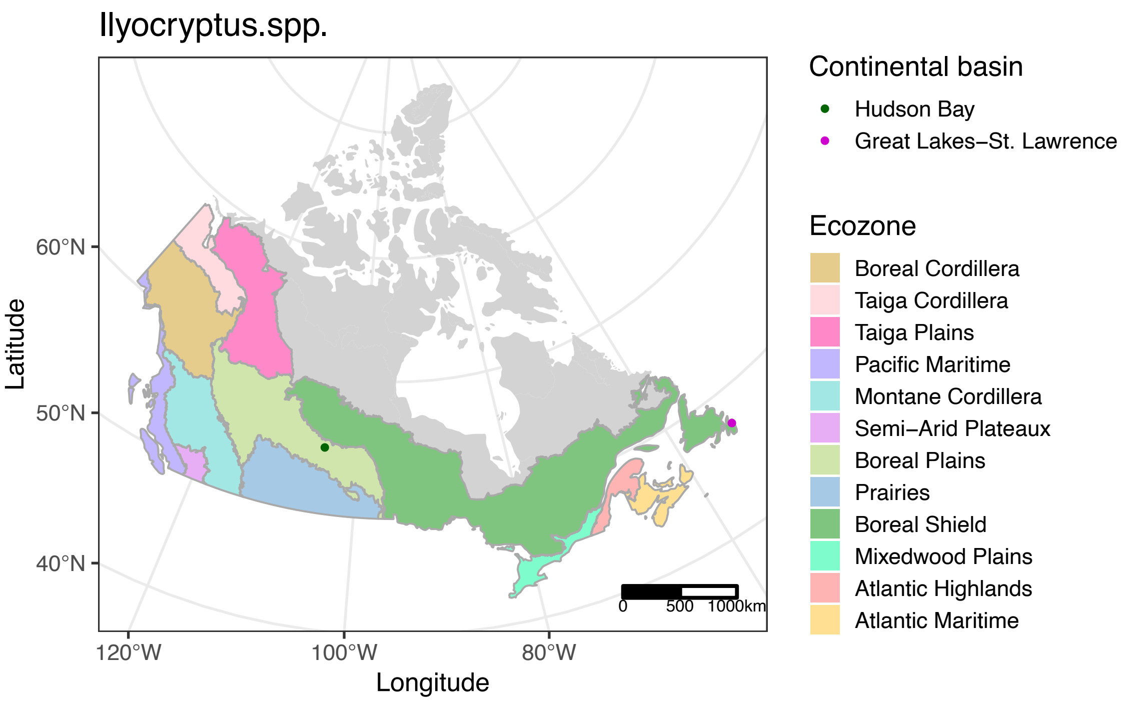
100°W
80°W
Longitude
0
500
1000km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100°W
80°W
Longitude
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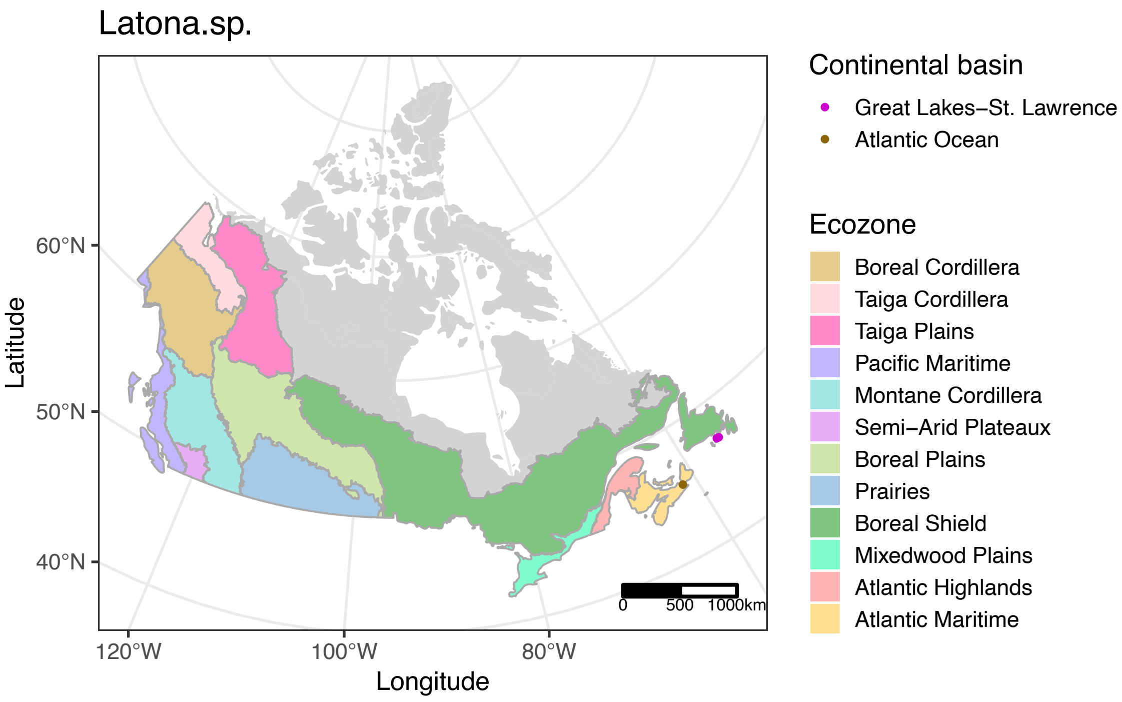
1000km
Continental basin
● Hudson Bay
● Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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100°W
80°W
Longitude
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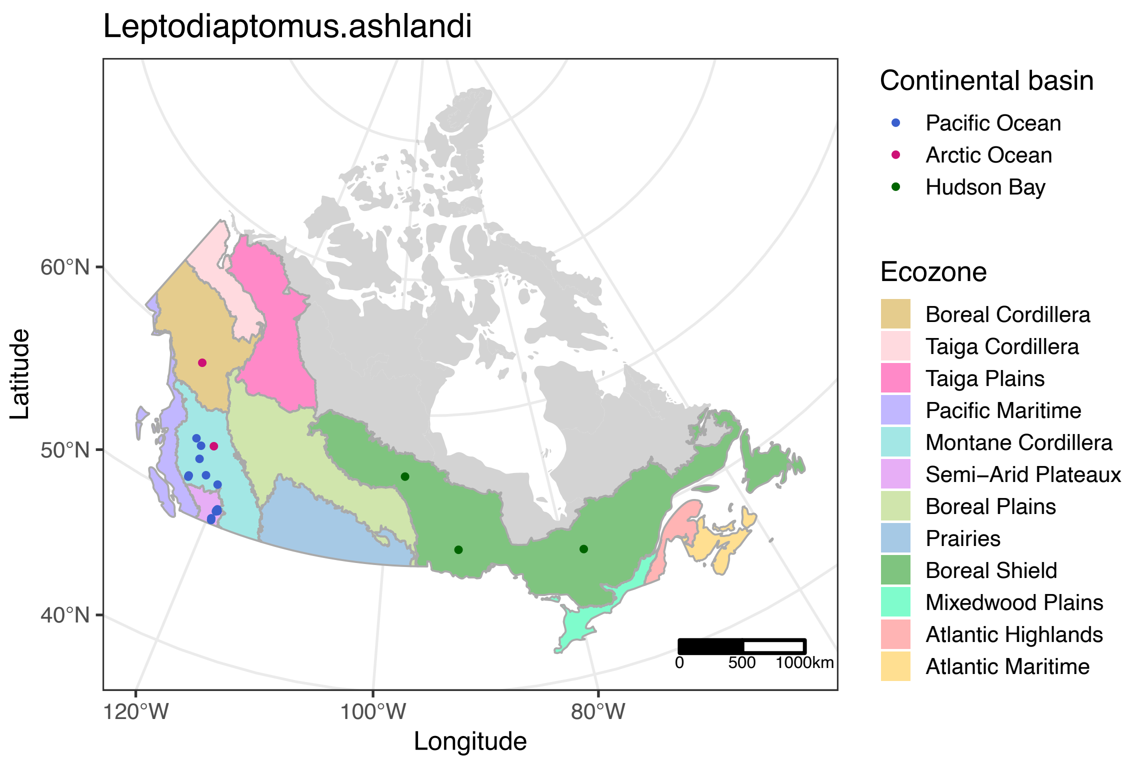
1000km
Continental basin
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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● Pacific Ocean
● Arctic Ocean
● Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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50°N
40°N
Latitude
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100°W
80°W
Longitude
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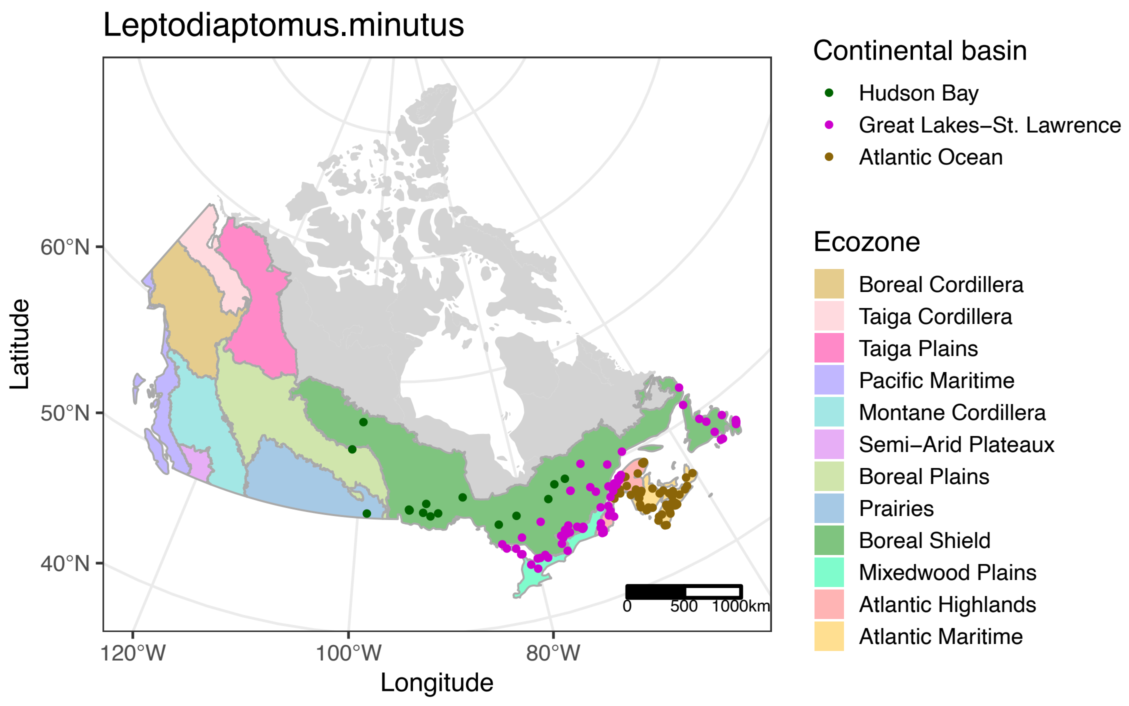
1000km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Continental basin
● Hudson Bay
● Great Lakes–St. Lawrence
● Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
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40°N
Latitude
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100°W
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Longitude
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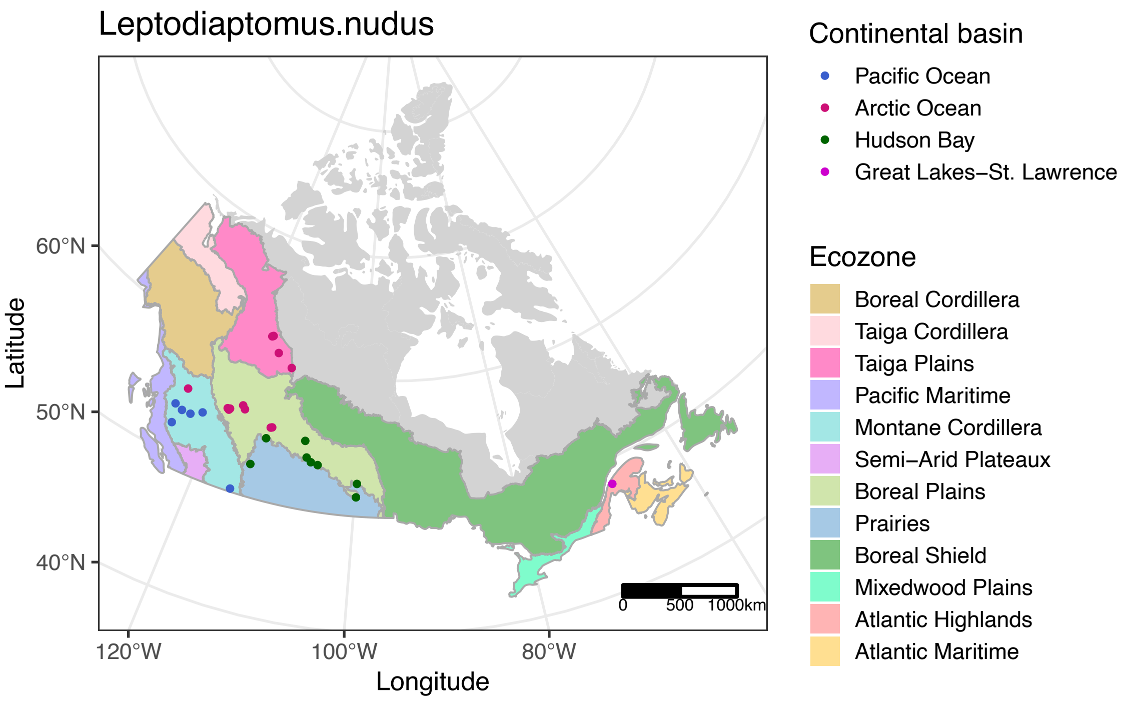
1000km



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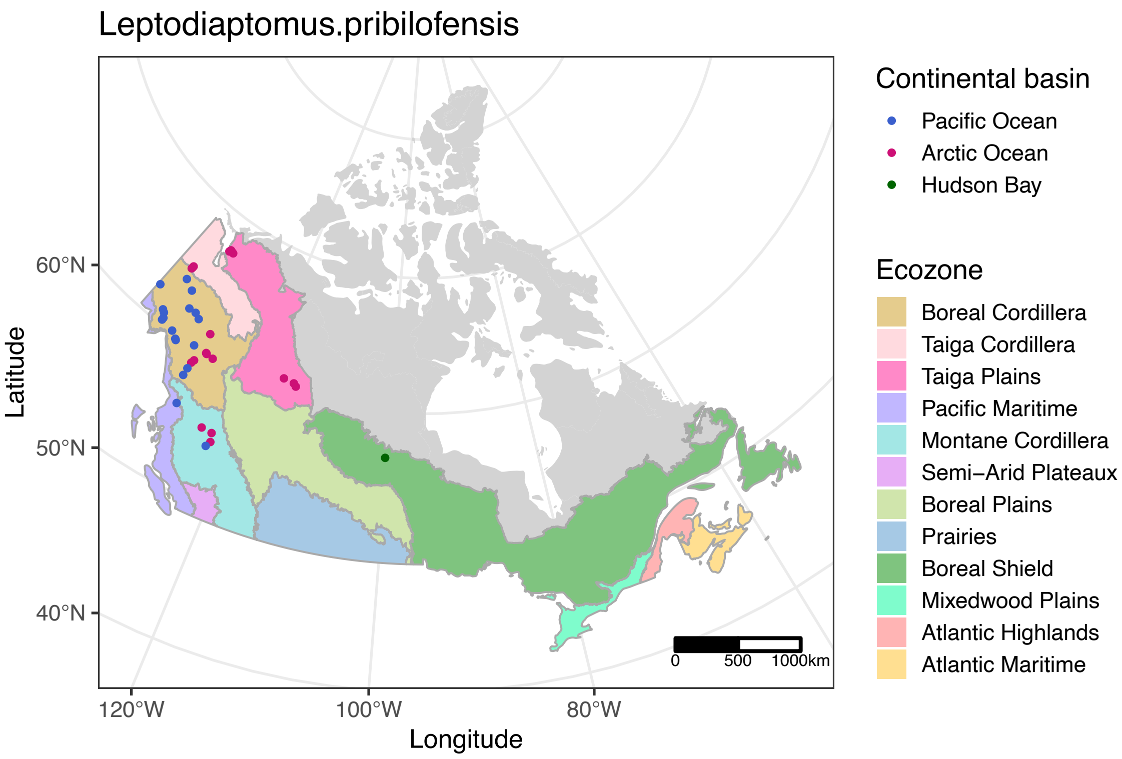
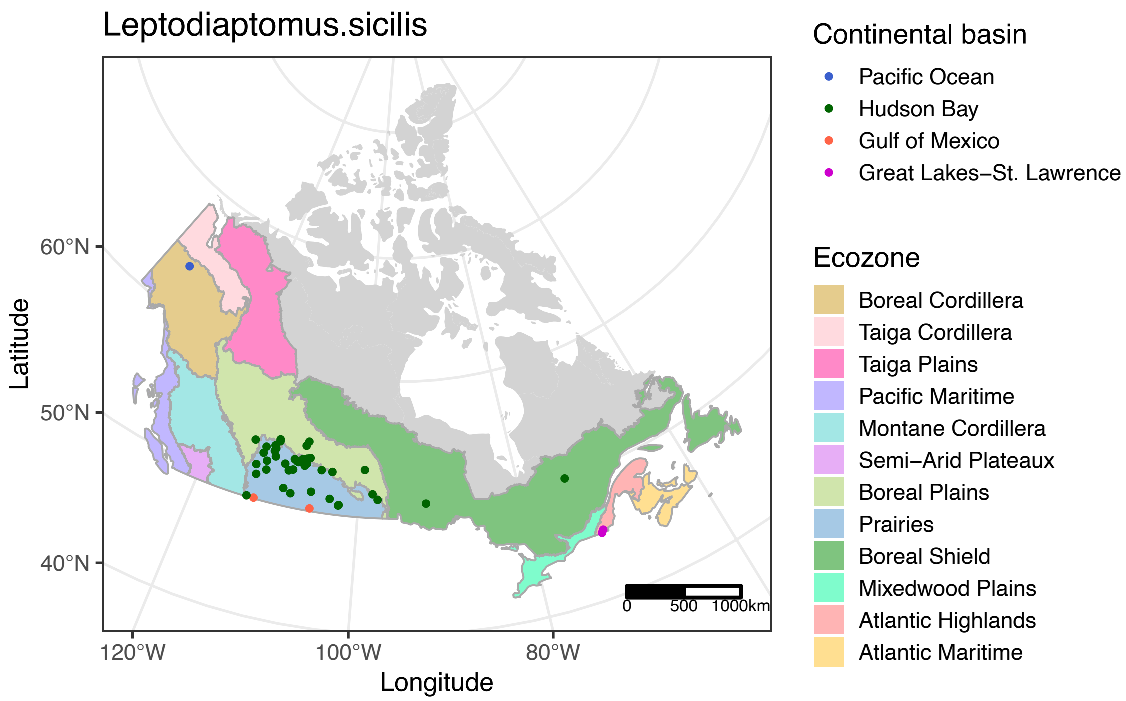


Leptodiaptomus.pribilofensis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Continental basin
Pacific Ocean
Hudson Bay
Gulf of Mexico
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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50°N
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Latitude
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100°W
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Longitude
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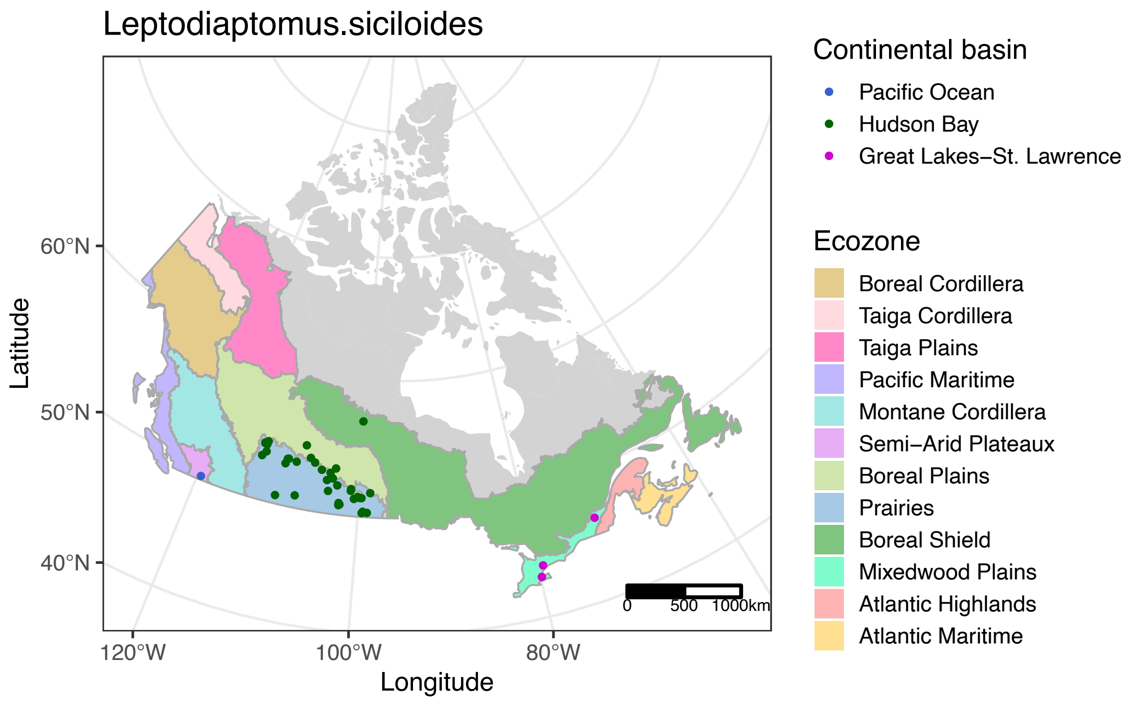
1000km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Continental basin
Pacific Ocean
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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Latitude
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100°W
80°W
Longitude
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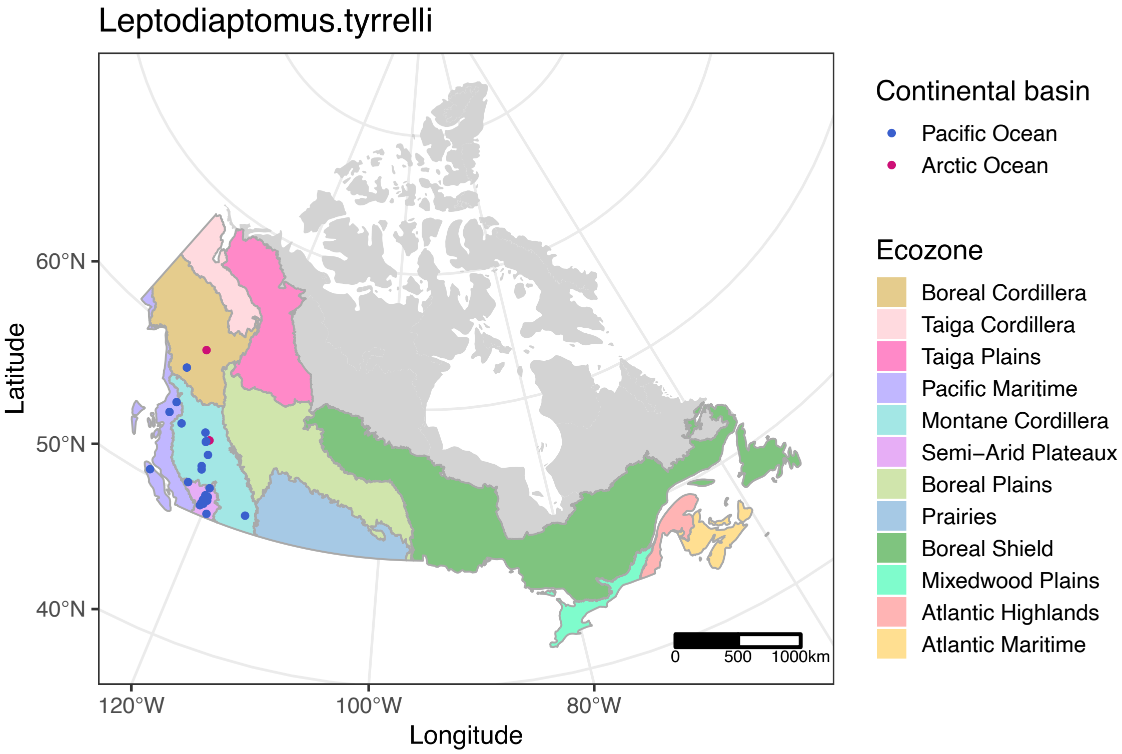
1000km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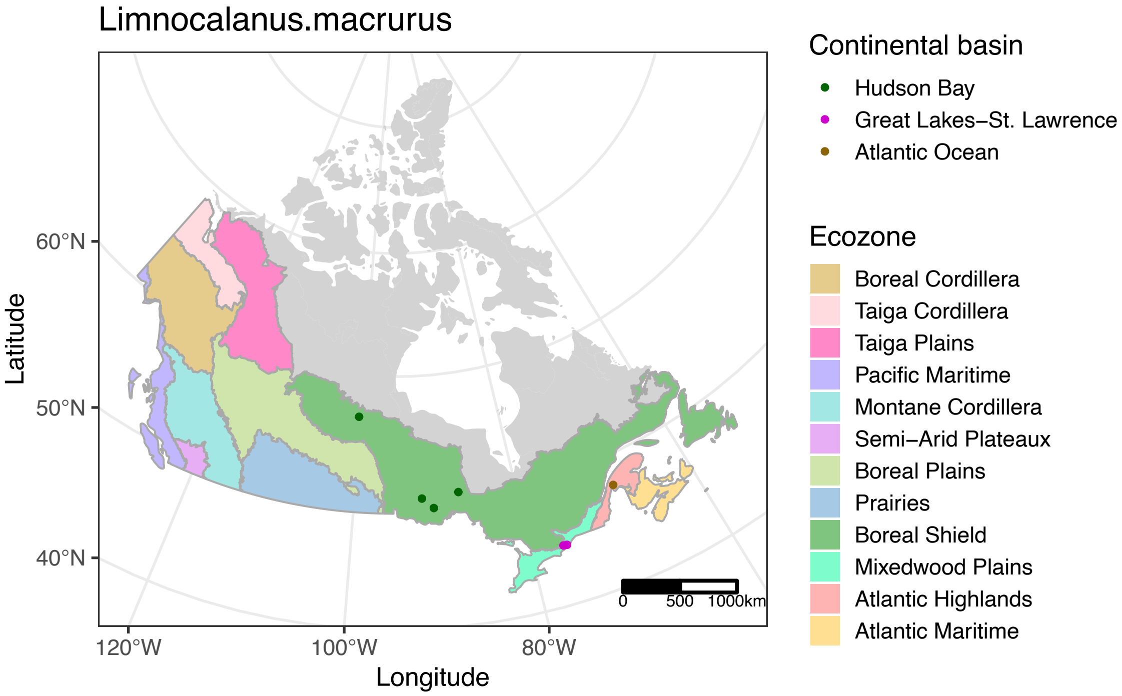
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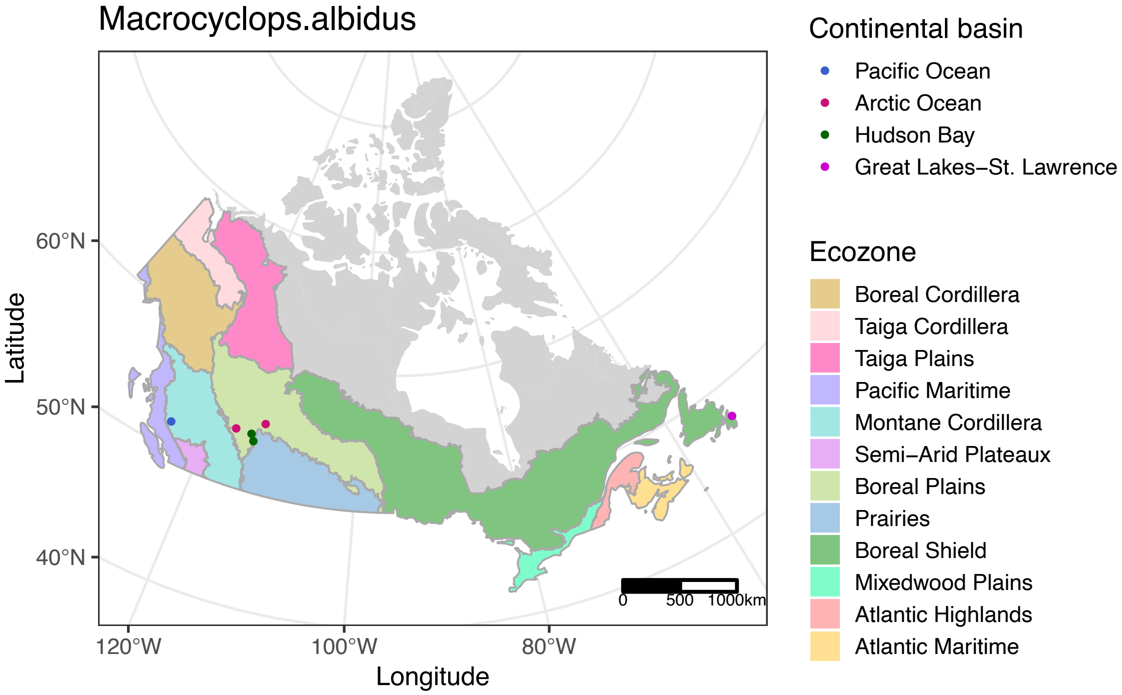
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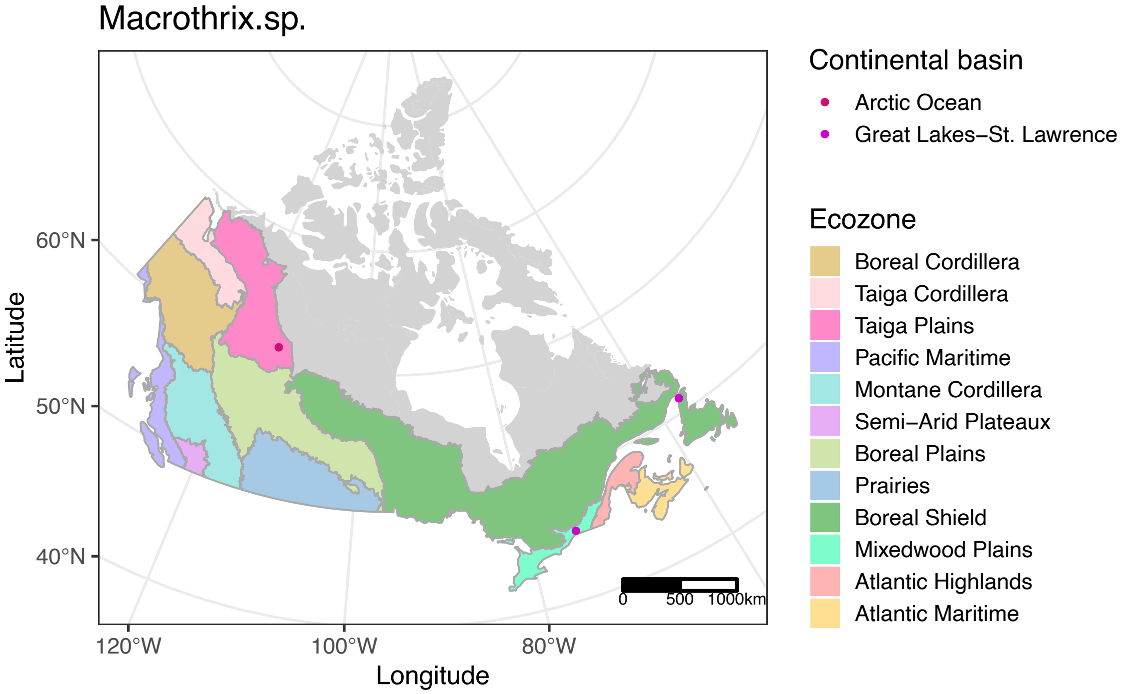
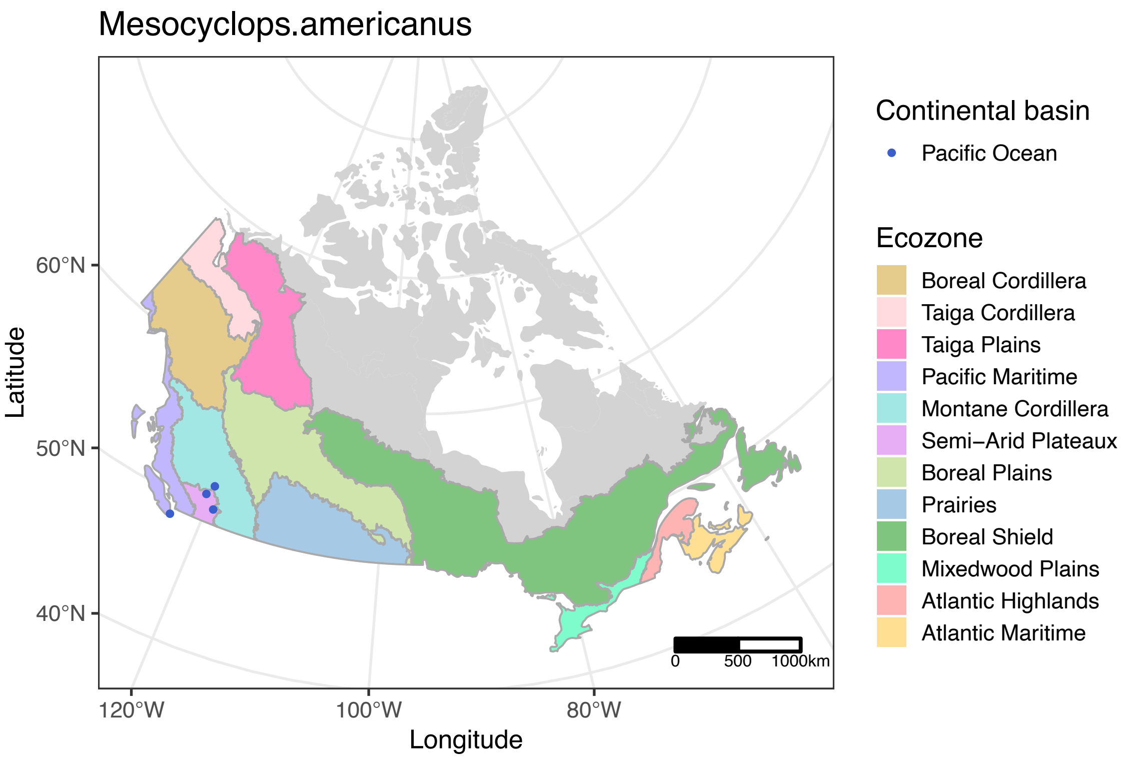

Macrothrix.sp.


Mesocyclops.americanus
Latitude
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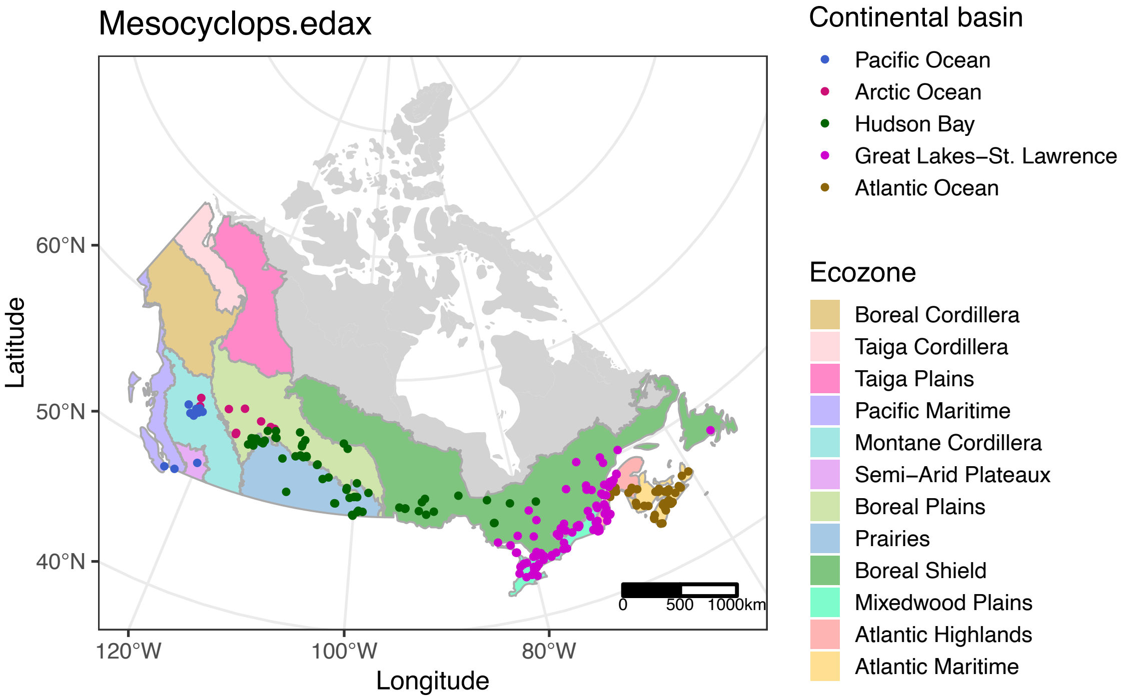
40°N
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
Pacific Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Mesocyclops.edax
Latitude
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100°W
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Longitude
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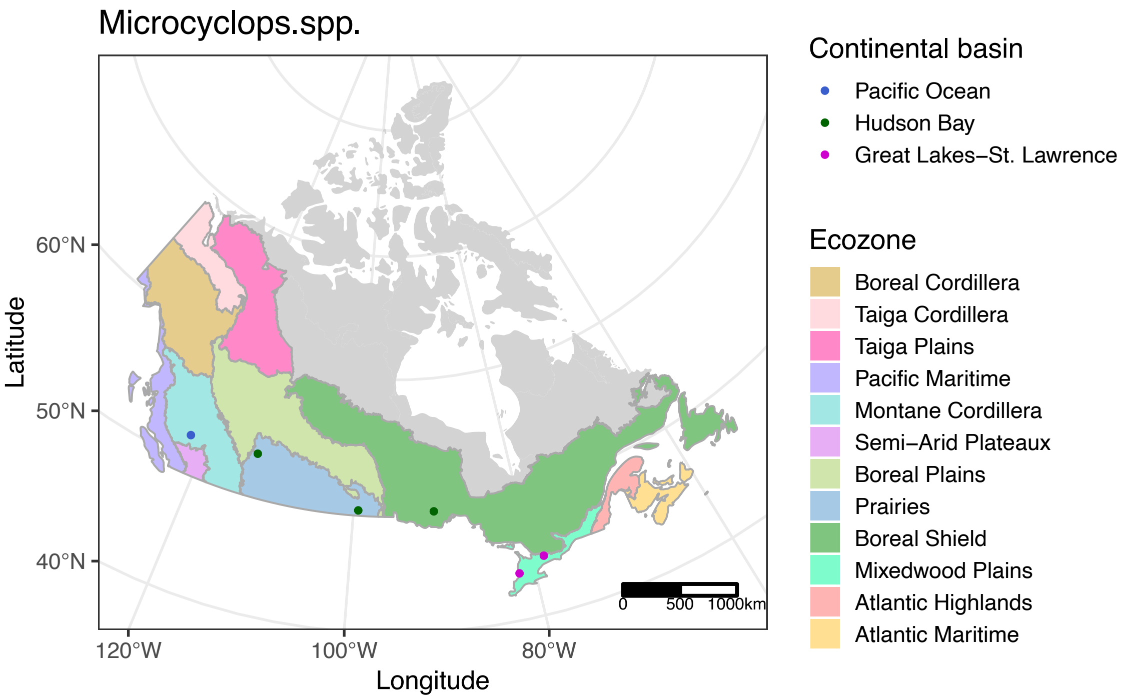
1000km
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Microcyclops.spp.
Continental basin
Pacific Ocean
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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50°N
40°N
Latitude
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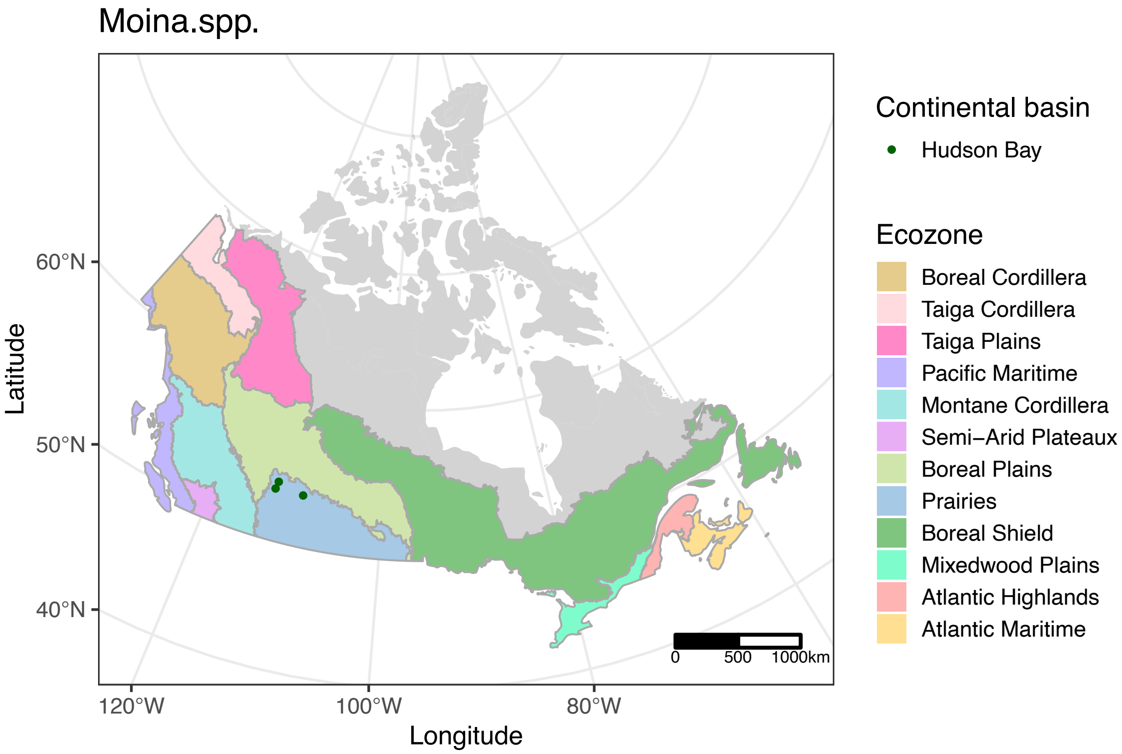
100°W
80°W
Longitude
0
500
1000km


Moina.spp.
Continental basin
Hudson Bay
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
60°N
50°N
40°N
Latitude
120°W
100°W
80°W
Longitude
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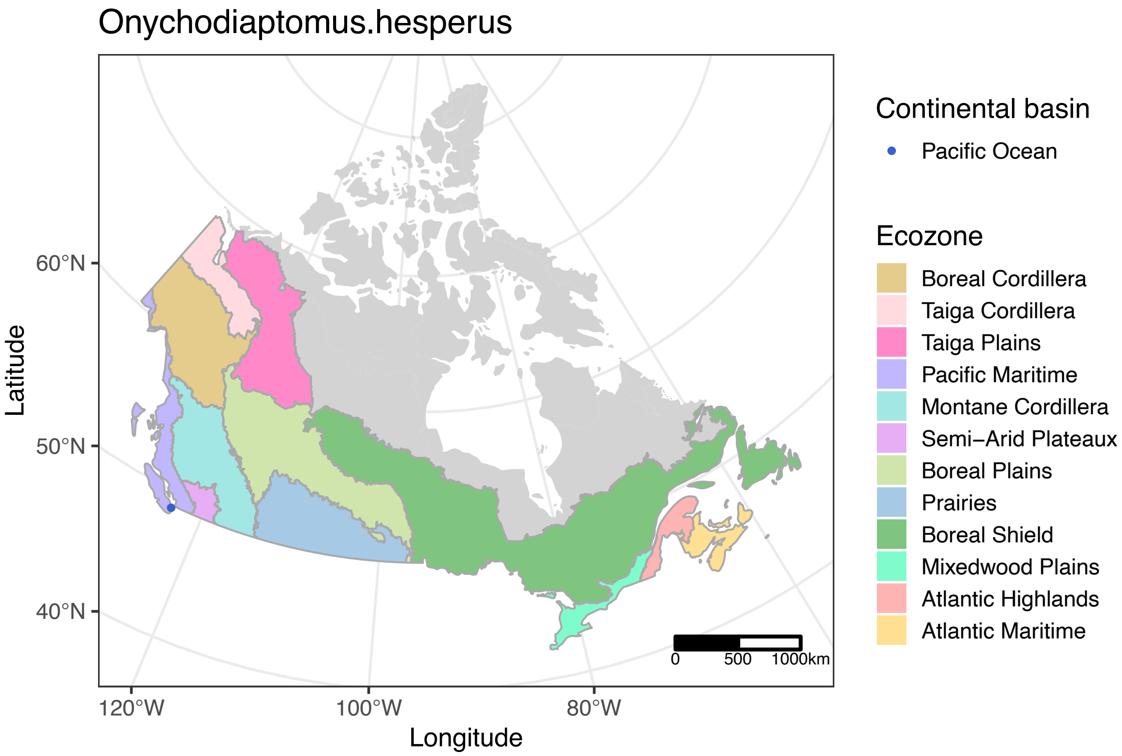
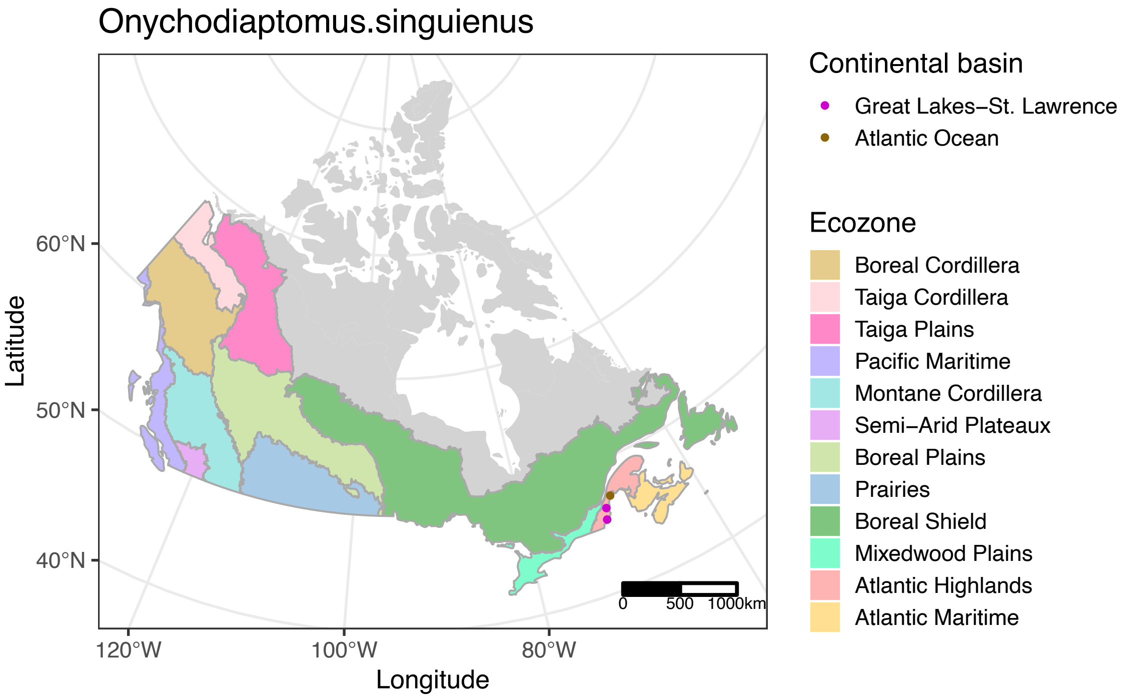
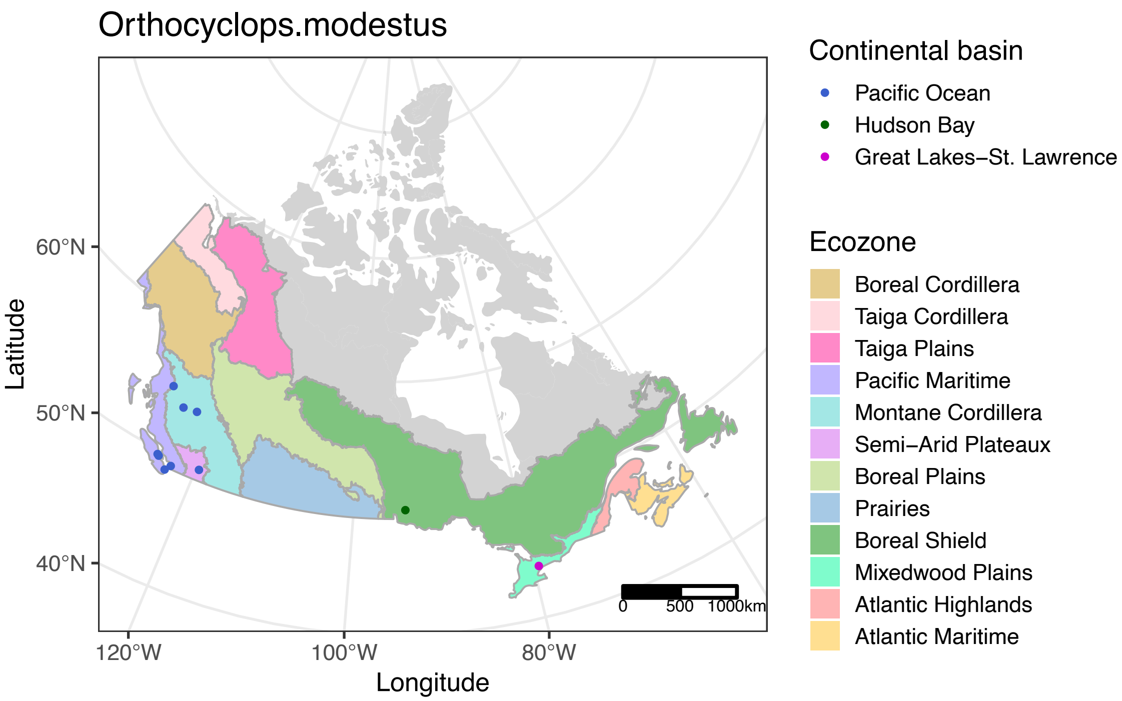
500
1000km



Onychodiaptomus.hesperus



Onychodiaptomus.singuienus


Orthocyclops.modestus
Continental basin
Pacific Ocean
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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Latitude
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100°W
80°W
Longitude
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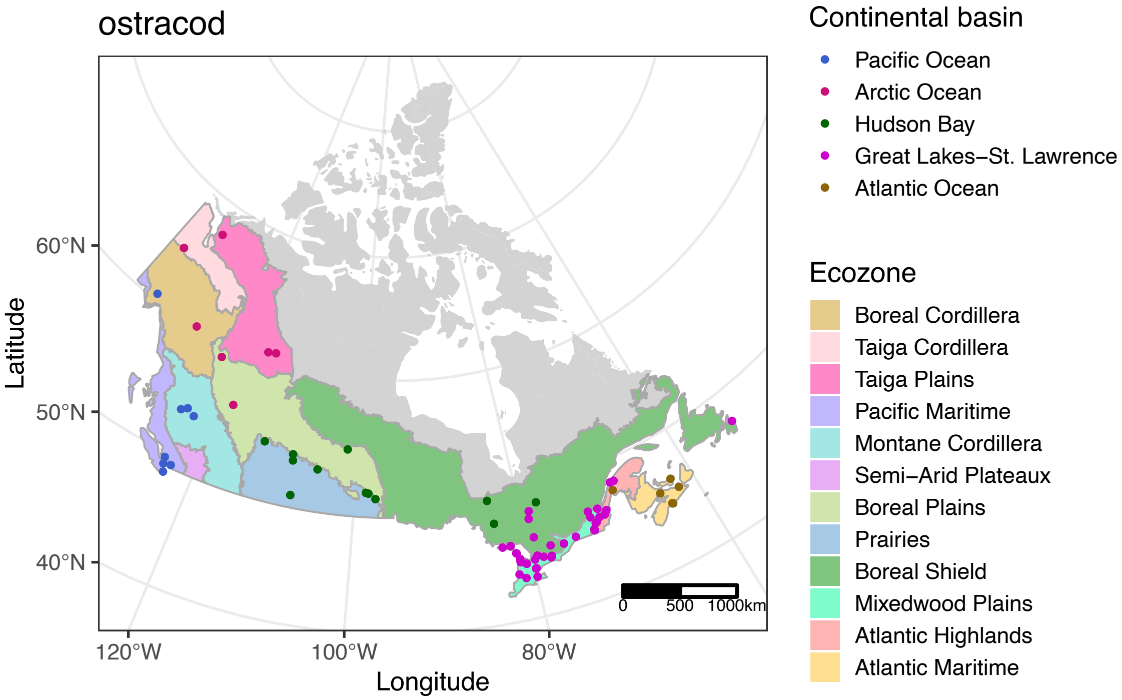
1000km


ostracod
Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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Latitude
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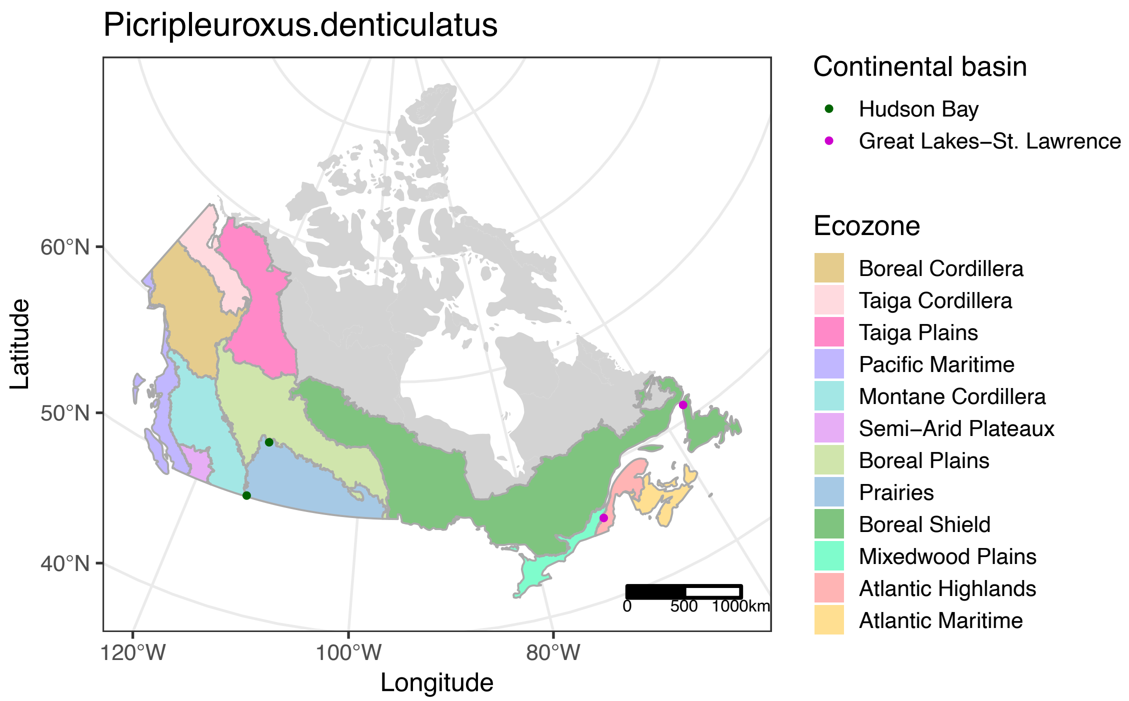
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Latitude
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1000km
Continental basin
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Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
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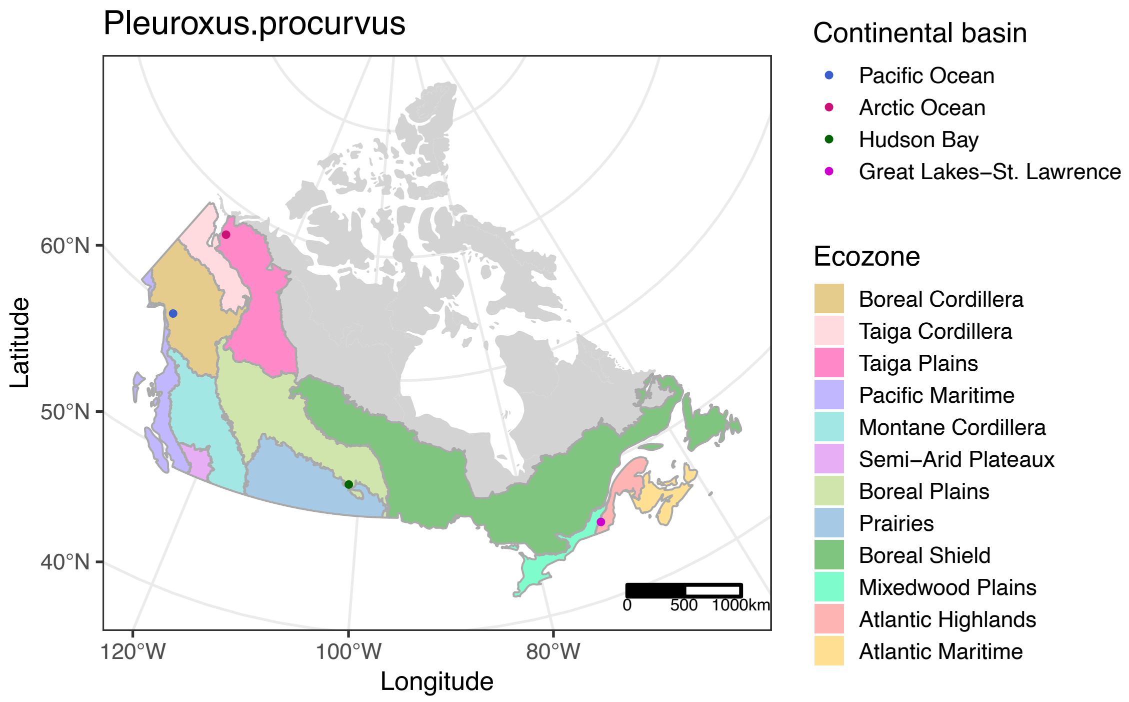
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime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Continental basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
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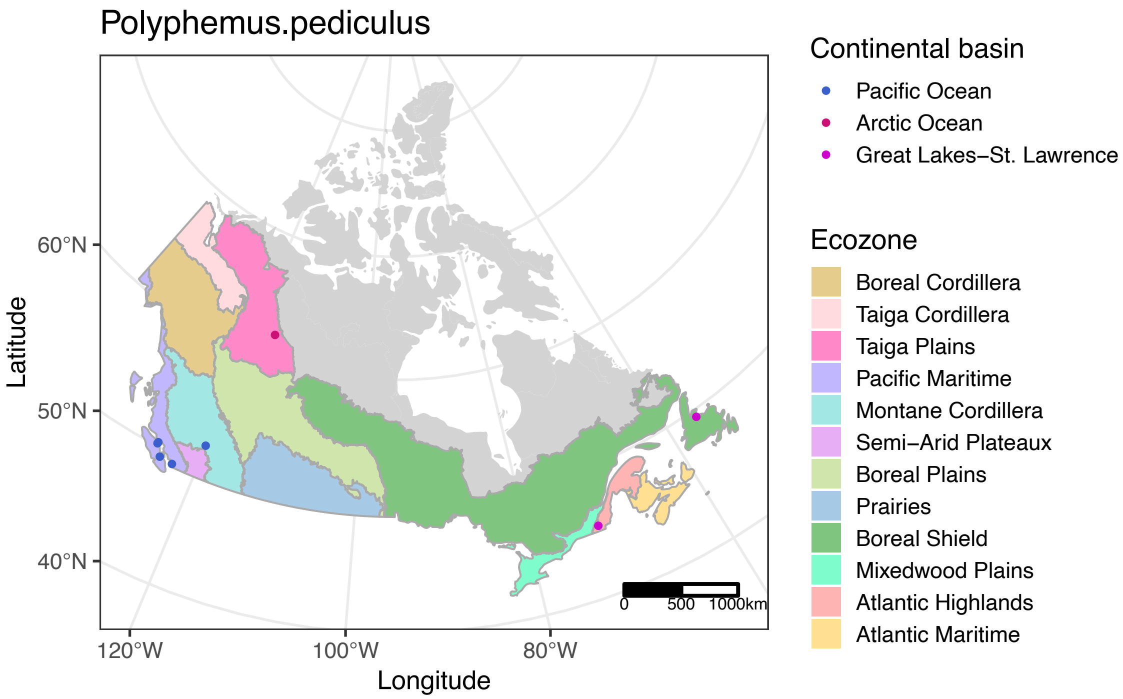
Atlantic Highlands
Atlantic Maritime


Polyphemus.pediculus
Continental basin
Pacific Ocean
Arctic Ocean
Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
Latitude
60°N
50°N
40°N
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100°W
80°W
Longitude
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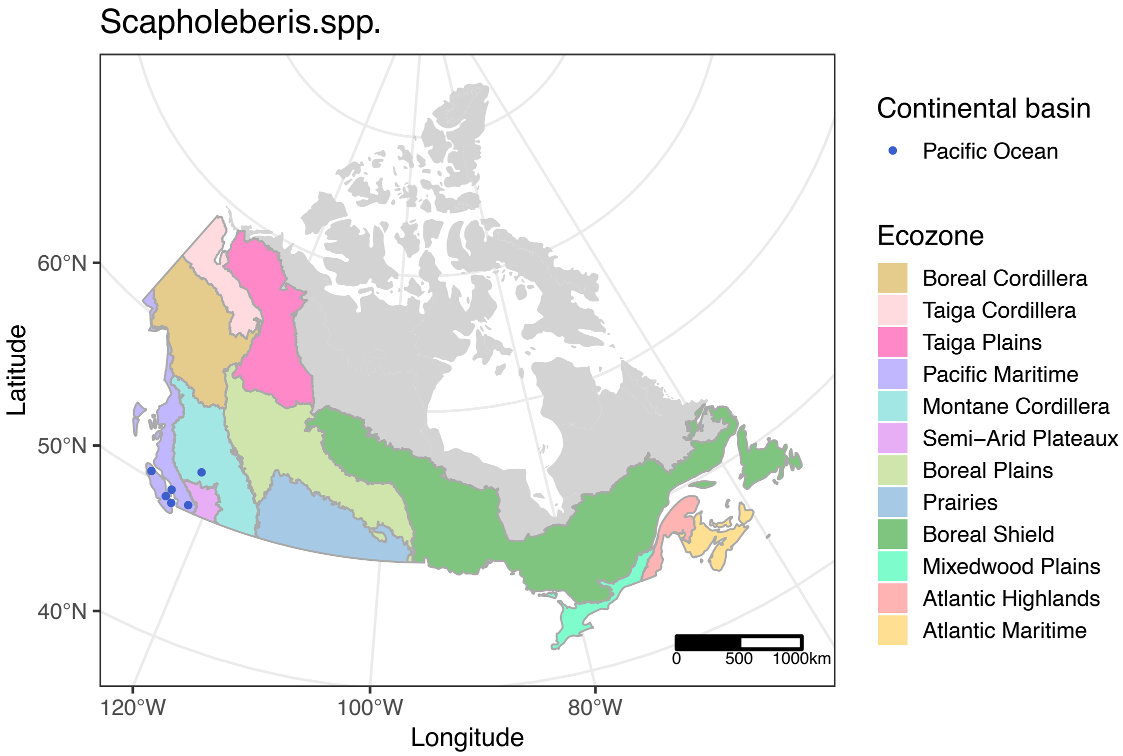
500
1000km


Scapholeberis.spp.
Continental basin
Pacific Ocean
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime
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50°N
40°N
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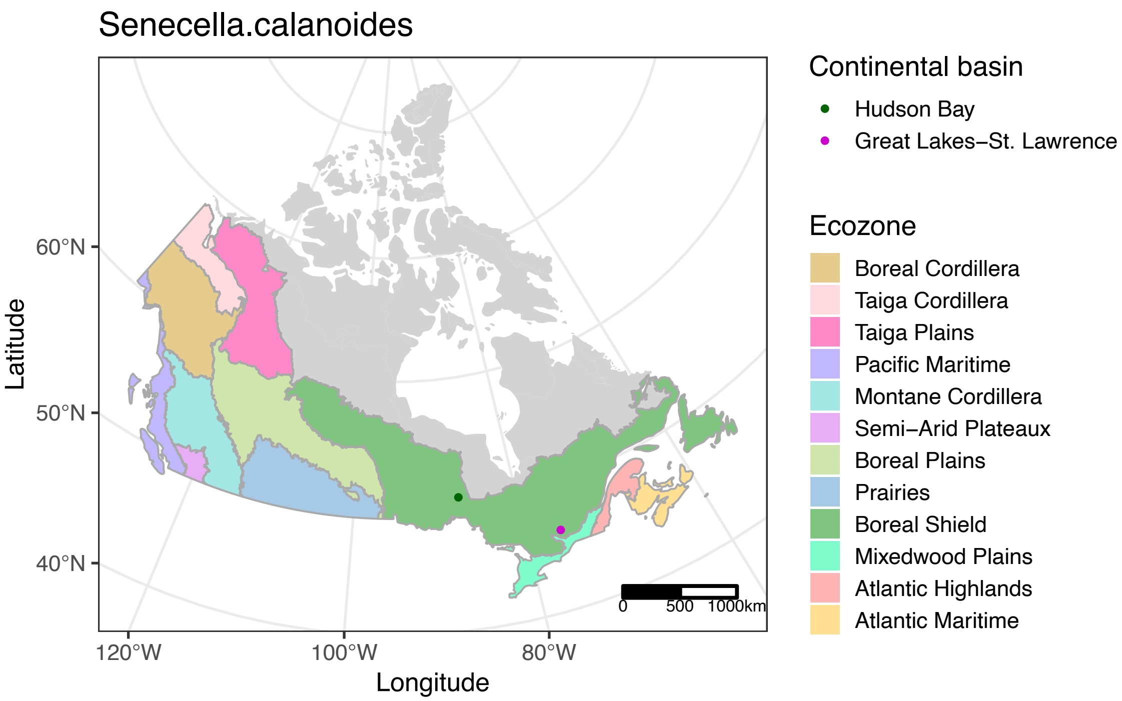
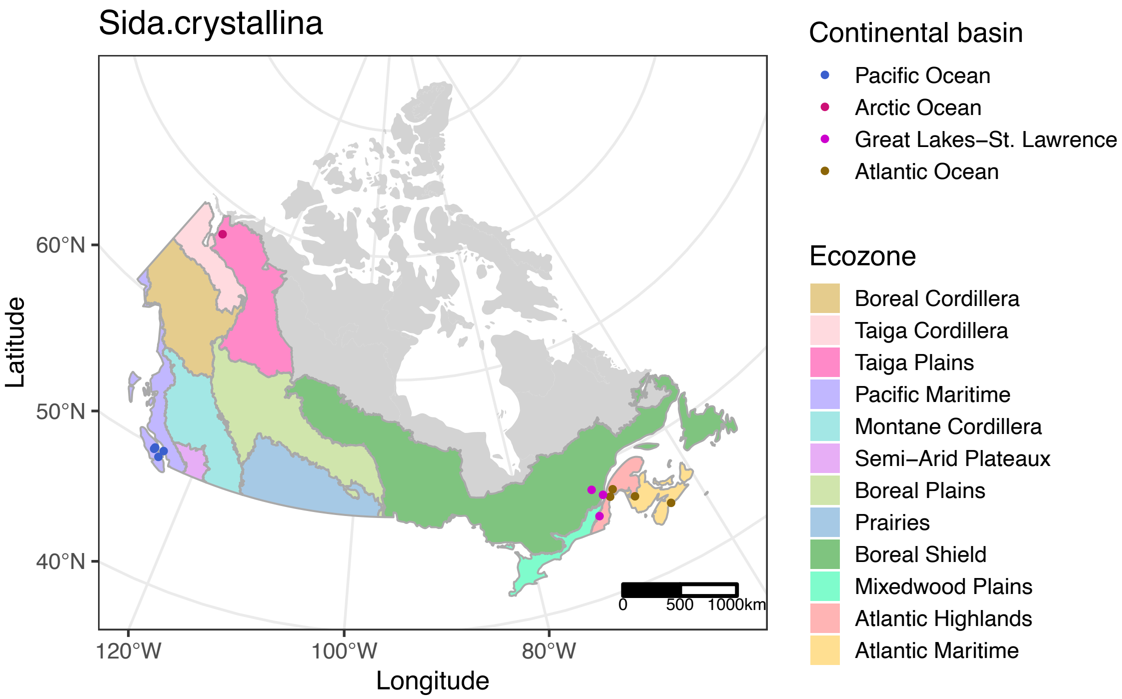
100°W
80°W
Longitude
0
500
1000km


Senecella.calanoides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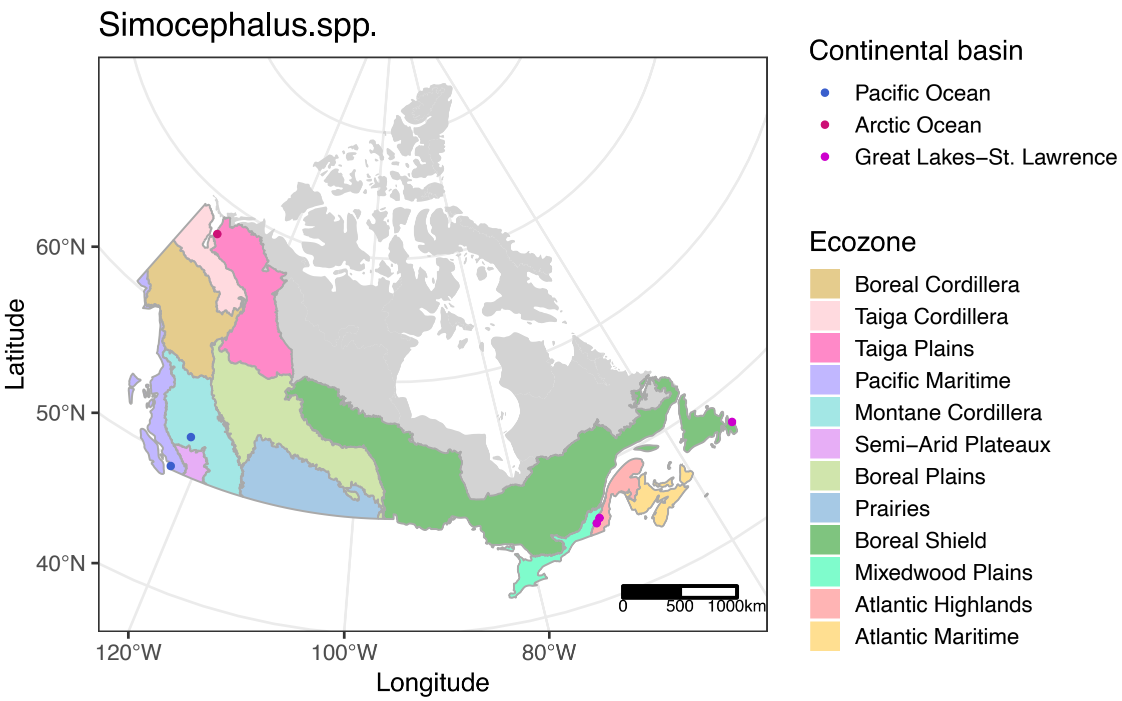
Simocephalus.spp.
Latitude
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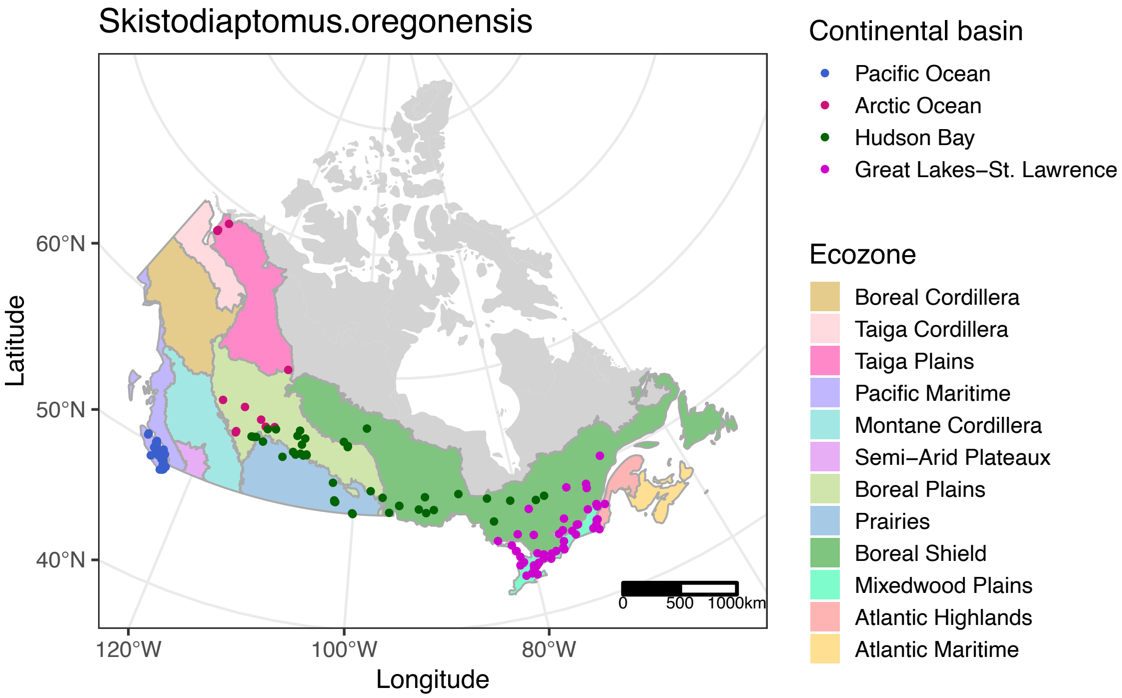
100°W
80°W
Longitude
0
500
1000km
Continental basin
● Pacific Ocean
● Arctic Ocean
● Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime


Skistodiaptomus.oregonensis
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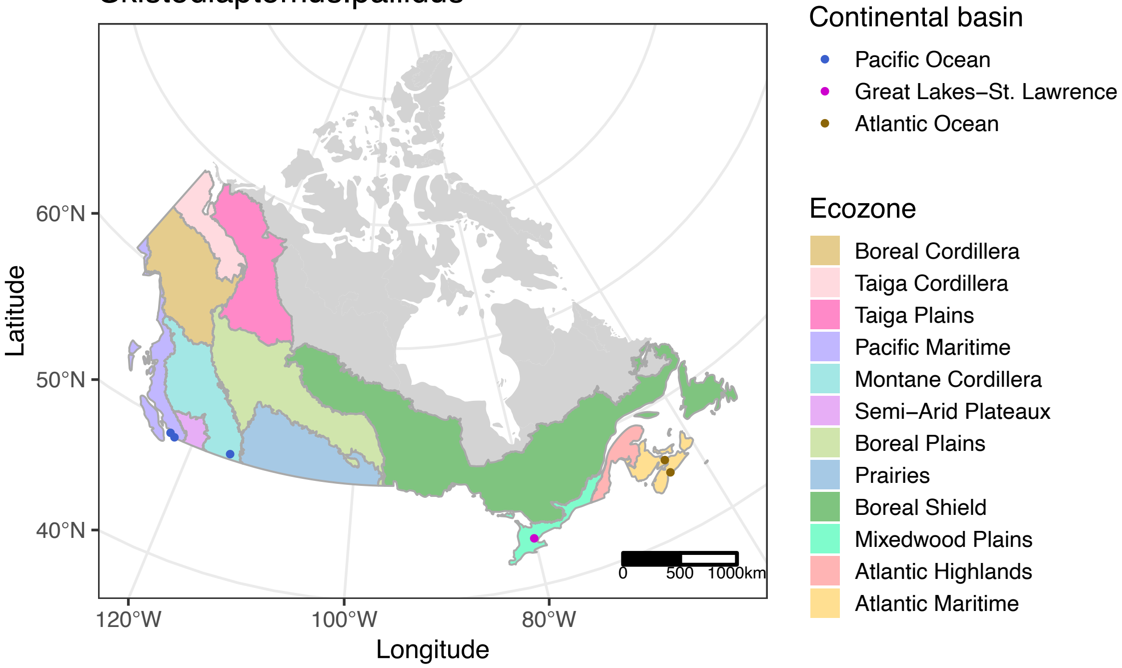
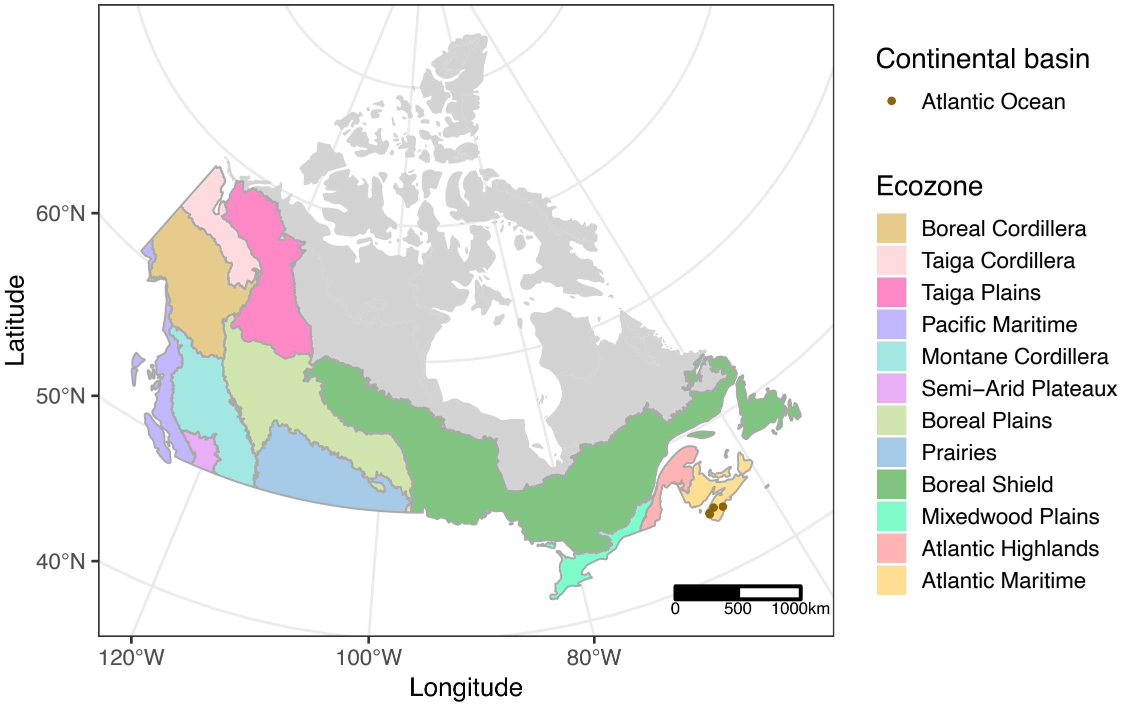
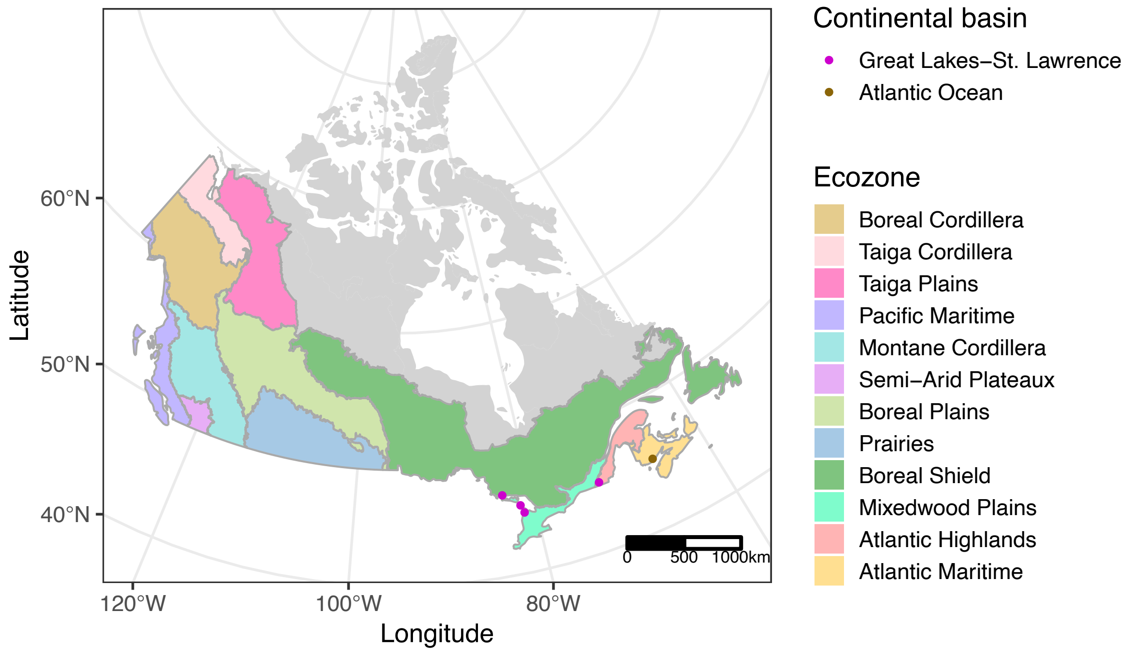
40°N
120°W
100°W
80°W
Longitude
0
500
1000km
Continental basin
● Pacific Ocean
● Arctic Ocean
● Hudson Bay
● Great Lakes–St. Lawrence
Ecozone
Boreal Cordillera
Taiga Cordillera
Taiga Plains
Pacific Maritime
Montane Cordillera
Semi–Arid Plateaux
Boreal Plains
Prairies
Boreal Shield
Mixedwood Plains
Atlantic Highlands
Atlantic Maritime

Skistodiaptomus.pallidus

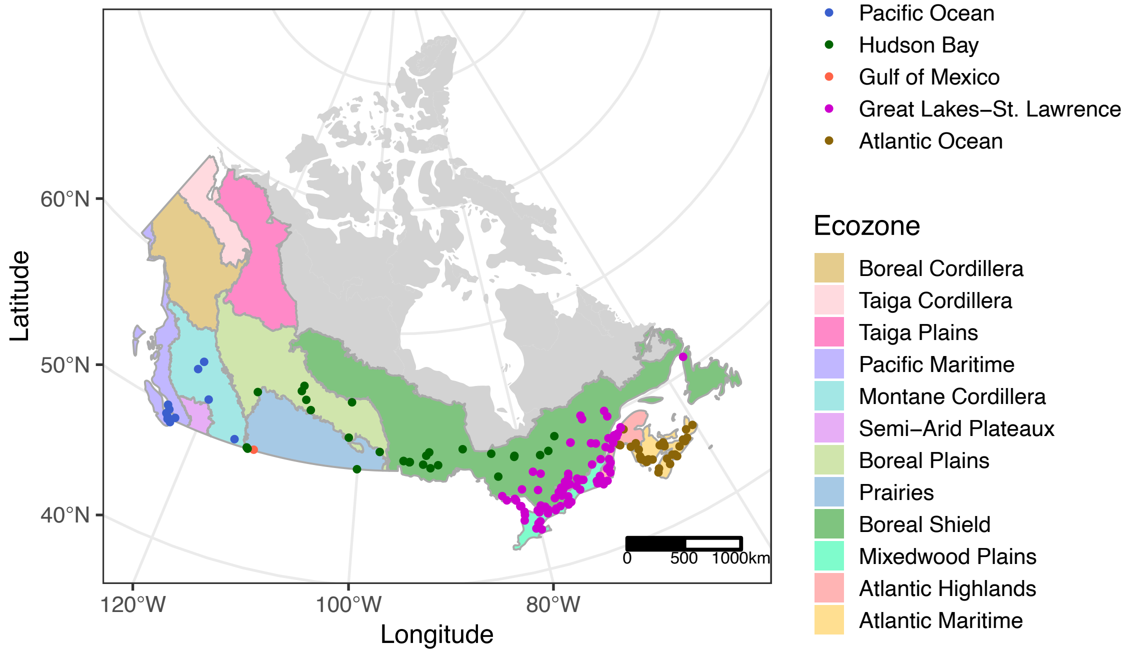


Skistodiaptomus.pygmaeus





Skistodiaptomus.reighardi



Tropocyclops.prasinus

ANNEXE E

TOTAL BIOMASS AND α-DIVERSITY

Table E.1 Total biomass (µg d.w./L), mean taxonomic and functional diversity values ± standard error by ecozone (a) and continental basin (b). Significant *p*-values from the ANOVA are shown. The largest values in each column are highlighted in bold.

(a) Ecozone	Total biomass	Shannon diversity	Evenness	Simpson diversity	Total richness	Rarefied richness	Functional evenness	Functional dispersion	Functional richness
All	374.4 ± 51.1	1.03 ± 0.02	0.56 ± 0.01	0.52 ± 0.01	6.55 ± 0.10	5.60 ± 0.08	0.45 ± 0.01	0.15 ± 0.00	0.81 ± 0.02
Boreal Cordillera	88.6 ± 14.1	0.93 ± 0.05	**0.68 ± 0.03**	0.53 ± 0.02	4.17 ± 0.22	3.67 ± 0.16	**0.57 ± 0.05**	**0.18 ± 0.01**	0.47 ± 0.07
Taiga Plains	42.8 ± 11.0	0.88 ± 0.09	0.52 ± 0.04	0.46 ± 0.05	5.40 ± 0.42	4.55 ± 0.33	0.47 ± 0.05	0.12 ± 0.01	0.81 ± 0.11
Pacific Maritime	90.9 ± 28.2	0.97 ± 0.06	0.55 ± 0.03	0.49 ± 0.03	5.96 ± 0.25	5.23 ± 0.20	0.48 ± 0.03	0.13 ± 0.01	0.78 ± 0.06
Montane Cordillera	169.7 ± 22.83	0.93 ± 0.05	0.54 ± 0.03	0.49 ± 0.03	5.79 ± 0.25	5.13 ± 0.22	0.43 ± 0.03	0.13 ± 0.01	0.69 ± 0.06
Semi-Arid Plateaux	227.7 ± 70.1	0.86 ± 0.08	0.53 ± 0.04	0.46 ± 0.04	5.00 ± 0.23	4.52 ± 0.20	0.50 ± 0.05	0.13 ± 0.01	0.56 ± 0.07
Boreal Plains	869.2 ± 251.0	0.98 ± 0.06	0.50 ± 0.03	0.49 ± 0.03	7.10 ± 0.25	6.13 ± 0.21	0.43 ± 0.03	0.14 ± 0.01	1.05 ± 0.07
Prairies	**1738.1 ± 341.89**	0.94 ± 0.05	0.55 ± 0.03	0.49 ± 0.03	5.73 ± 0.21	5.05 ± 0.19	0.44 ± 0.03	0.14 ± 0.01	0.86 ± 0.07
Boreal Shield	89.1 ± 15.7	**1.20 ± 0.05**	0.59 ± 0.02	**0.58 ± 0.02**	**7.99 ± 0.29**	**6.76 ± 0.25**	0.46 ± 0.02	**0.17 ± 0.01**	0.81 ± 0.05
Mixedwood Plains	148.2 ± 51.3	**1.24 ± 0.06**	0.60 ± 0.02	**0.60 ± 0.02**	**8.02 ± 0.28**	**6.59 ± 0.25**	0.45 ± 0.03	**0.17 ± 0.01**	**1.11 ± 0.07**
Atlantic Highlands	117.3 ± 46.4	**1.22 ± 0.05**	0.59 ± 0.02	**0.60 ± 0.02**	**7.90 ± 0.3**	**6.46 ± 0.25**	0.43 ± 0.03	**0.17 ± 0.01**	0.89 ± 0.05
Atlantic Maritime	86.9 ± 11.7	0.90 ± 0.06	0.50 ± 0.03	0.45 ± 0.03	6.13 ± 0.28	5.15 ± 0.22	0.44 ± 0.03	0.12 ± 0.01	0.63 ± 0.05
p-value	<2e-16	<.0001	0.003	<.0001	<2e-16	<2e-16	NS	<.0001	<.0001

(b) **Continental basin**	**Total biomass**	**Shannon diversity**	**Evenness**	**Simpson diversity**	**Total richness**	**Rarefied richness**	**Functional evenness**	**Functional dispersion**	**Functional richness**
All	374.4 ± 51.1	1.03 ± 0.02	0.56 ± 0.01	0.52 ± 0.01	6.55 ± 0.1	5.6 ± 0.08	0.45 ± 0.01	0.15 ± 0.00	0.81 ± 0.02
Pacific Ocean	147.7 ± 18.8	0.91 ± 0.03	0.55 ± 0.02	0.48 ± 0.02	5.46 ± 0.14	4.85 ± 0.12	**0.47 ± 0.02**	0.13 ± 0.01	0.67 ± 0.04
Arctic Ocean	388.5 ± 217.2	0.95 ± 0.06	0.55 ± 0.03	0.49 ± 0.03	5.86 ± 0.27	5.01 ± 0.23	0.45 ± 0.03	0.14 ± 0.01	0.84 ± 0.07
Hudson Bay	**1091.0 ± 185.1**	1.04 ± 0.04	0.56 ± 0.02	0.52 ± 0.02	6.87 ± 0.21	5.94 ± 0.18	0.46 ± 0.02	0.15 ± 0.01	**0.95 ± 0.04**
Great Lakes-St. Lawrence	128.9 ± 27.4	**1.20 ± 0.03**	**0.58 ± 0.01**	**0.59 ± 0.01**	**7.94 ± 0.18**	**6.55 ± 0.15**	0.44 ± 0.02	**0.16 ± 0.00**	0.92 ± 0.04
Atlantic Ocean	79.5 ± 9.8	0.98 ± 0.05	0.53 ± 0.02	0.49 ± 0.02	6.4 ± 0.25	5.37 ± 0.21	0.44 ± 0.03	0.13 ± 0.01	0.67 ± 0.05
p-value	<.0001	<.0001	NS	<.0001	<2e-16	<.0001	NS	<.0001	<.0001

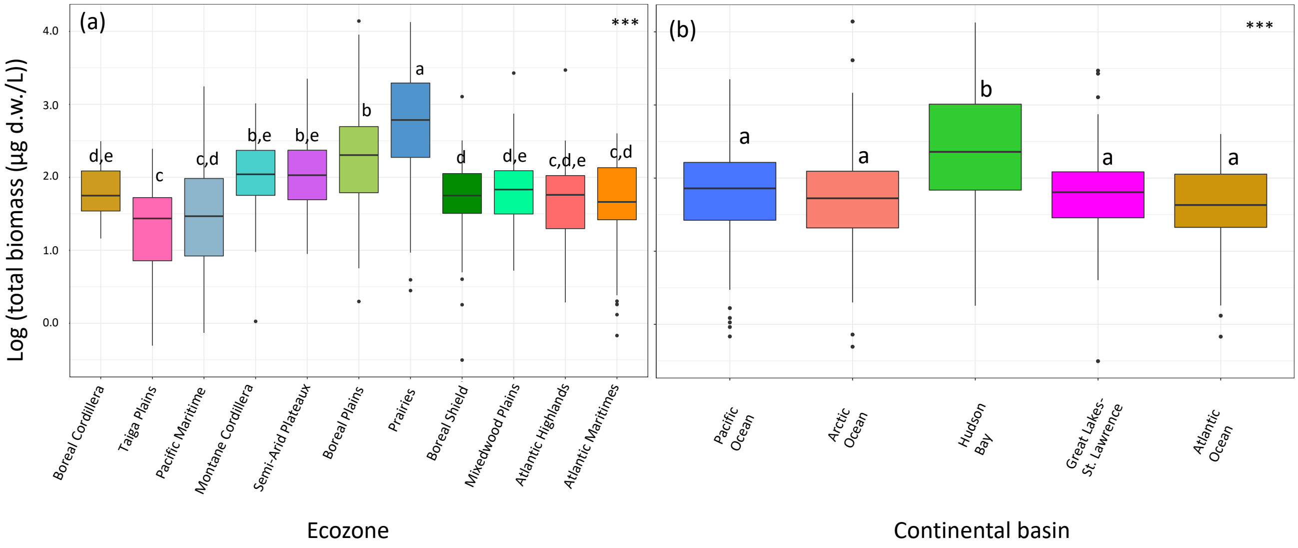


Figure E.2 Mean total biomass (± SE) across ecozones (a) and continental basins (b). Note that the y-axis scale varies between panels. Boxes that share the same letter are not significantly different. **p*-value<0.05; ***p*-value<0.01; ****p*-value<0.001

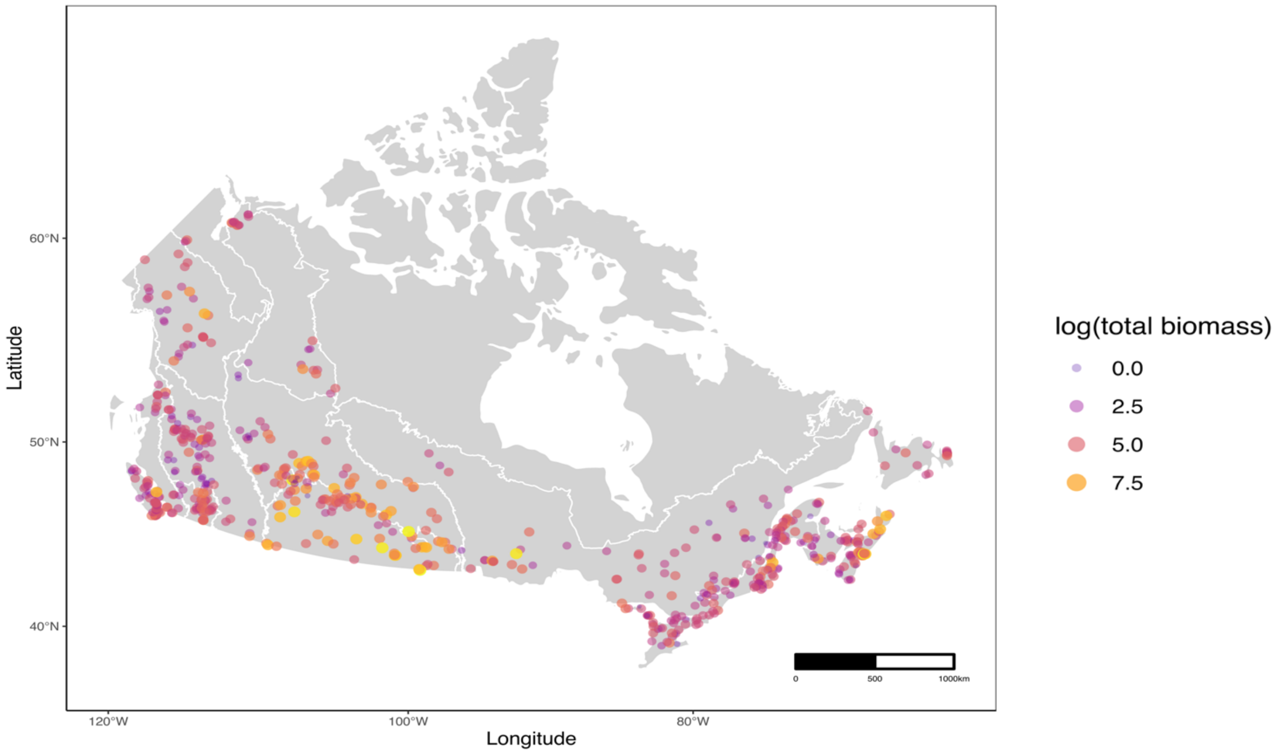


Figure E.3 Heatmap of total crustacean zooplankton biomass ($\log_{10}$ transformed) by ecozone (delimited in white). The map was created using Canada Atlas Lambert projection (NAD83 CSRS).

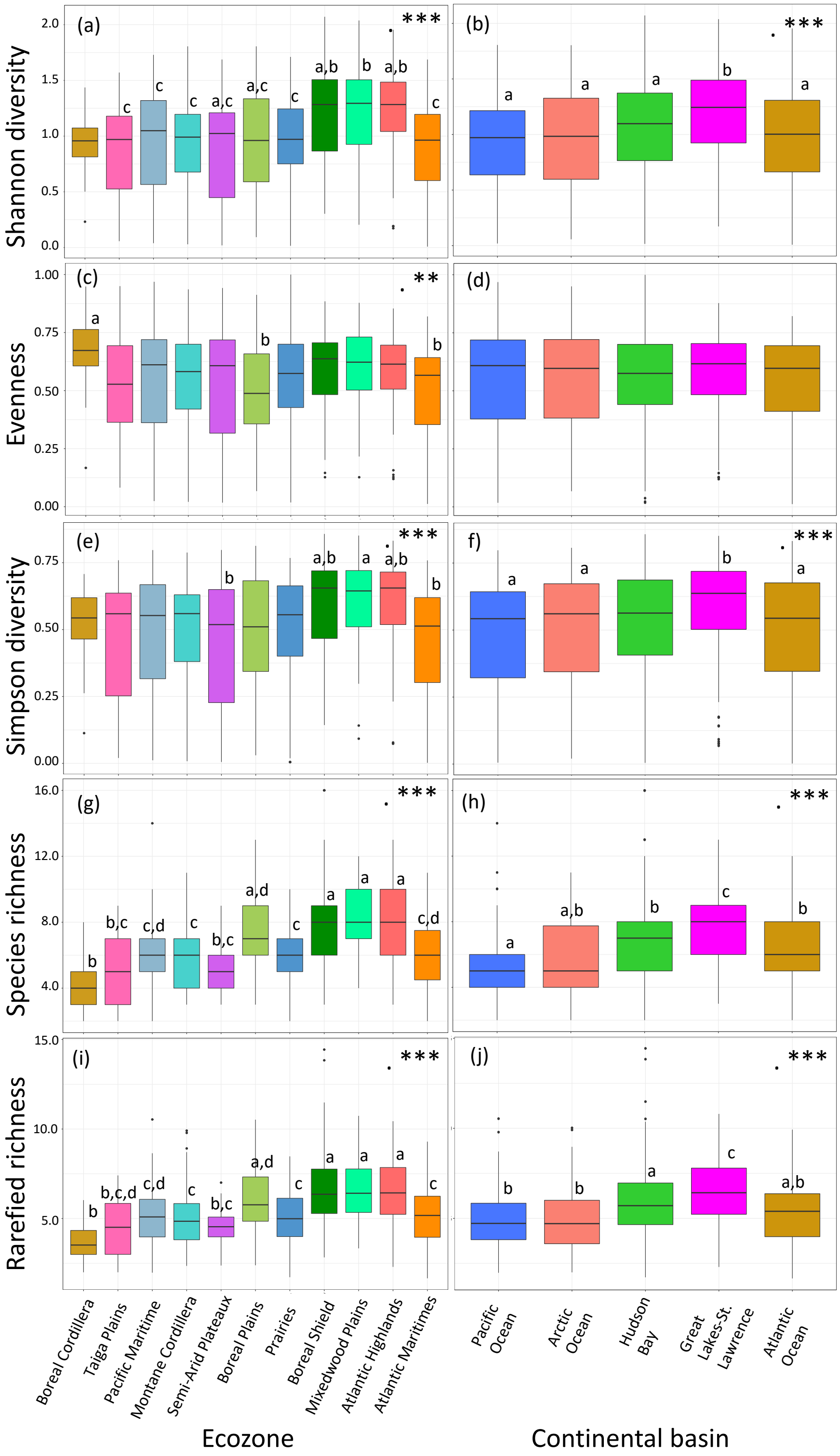


Figure E.4 Taxonomic diversity indices: Shannon diversity (a,b), evenness (c,d), Simpson's diversity (e,f), richness (g,h), rarefied richness (i,j) means (± SE across ecozones and continental basins respectively). Note that the y-axis scale varies between panels. Boxes that share the same letter are not significantly different. **p*-value<0.05; ***p*-value<0.01; ****p*-value<0.001

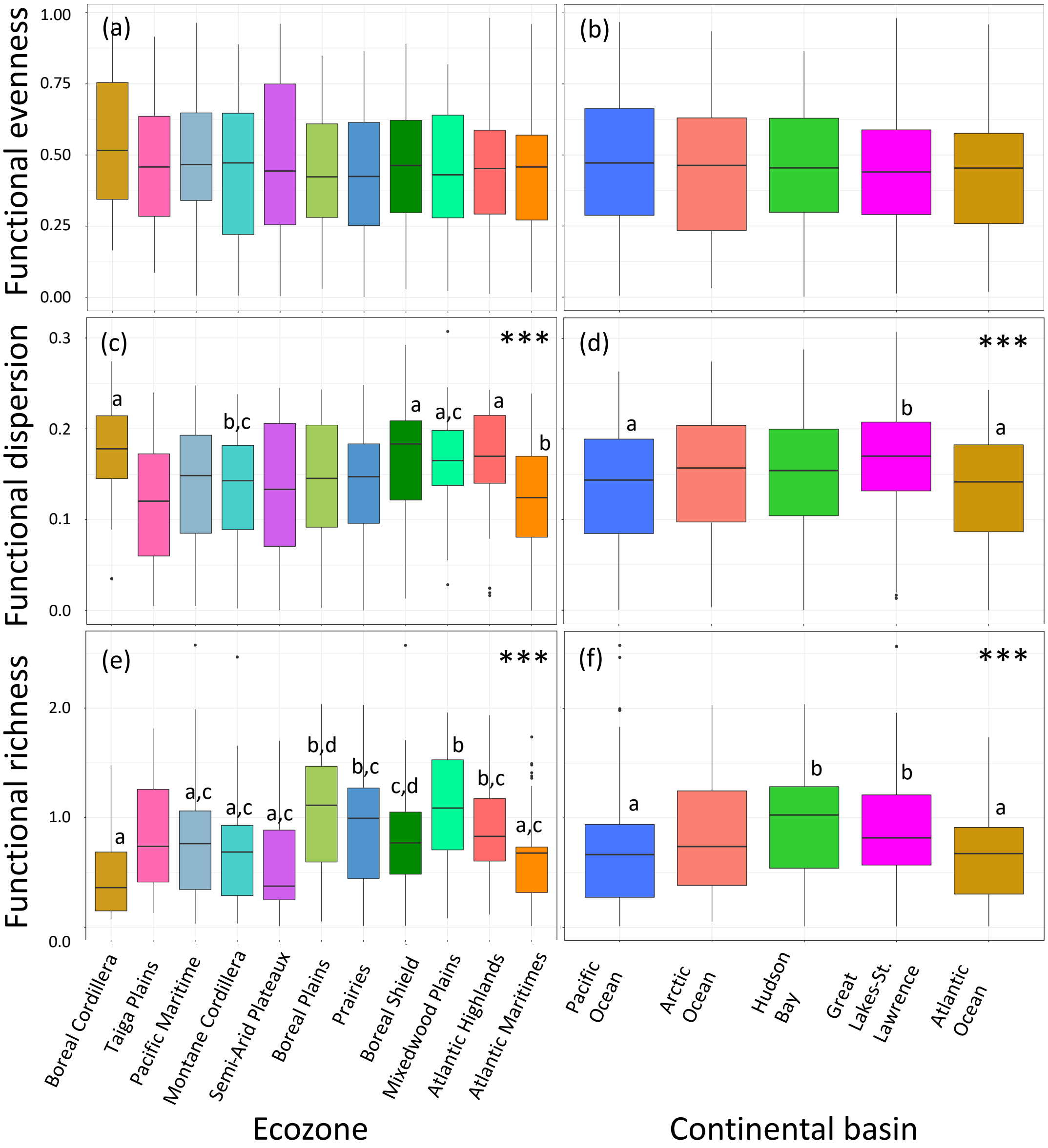


Figure E.5 Functional diversity indices: functional evenness (a,b), functional dispersion (c,d) and functional richness (e,f) means (± SE across ecozones and continental basins respectively). Note that the y-axis scale varies between panels. Boxes that share the same letter are not significantly different. **p*-value<0.05; ***p*-value<0.01; ****p*-value<0.001

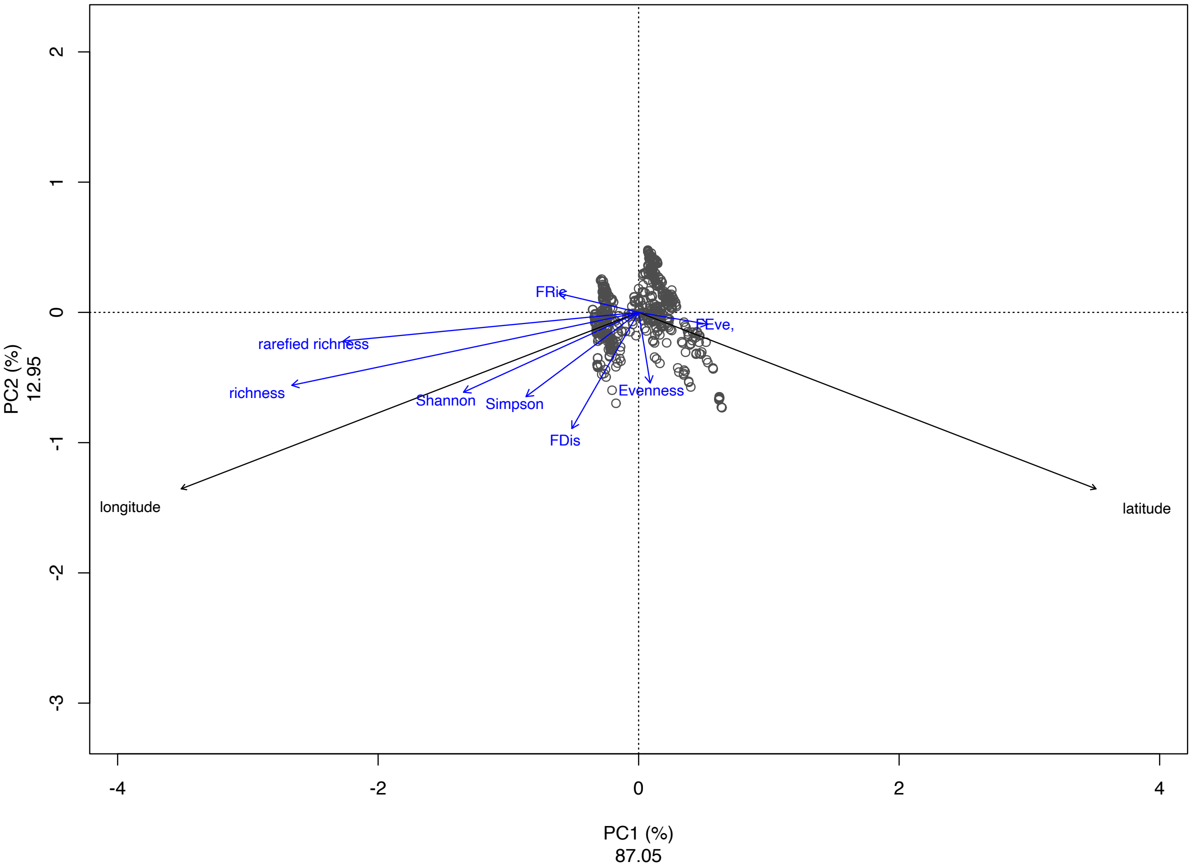


Figure E.6 Spatial patterns in α-diversity. PCA ordination plot (scaling 2) of lake longitude and latitude with α-diversity indices plotted passively. Only lakes where all diversity indices could be calculated are illustrated (n=613)

ANNEXE F

SPECIES RANK-FREQUENCY OCCURRENCES

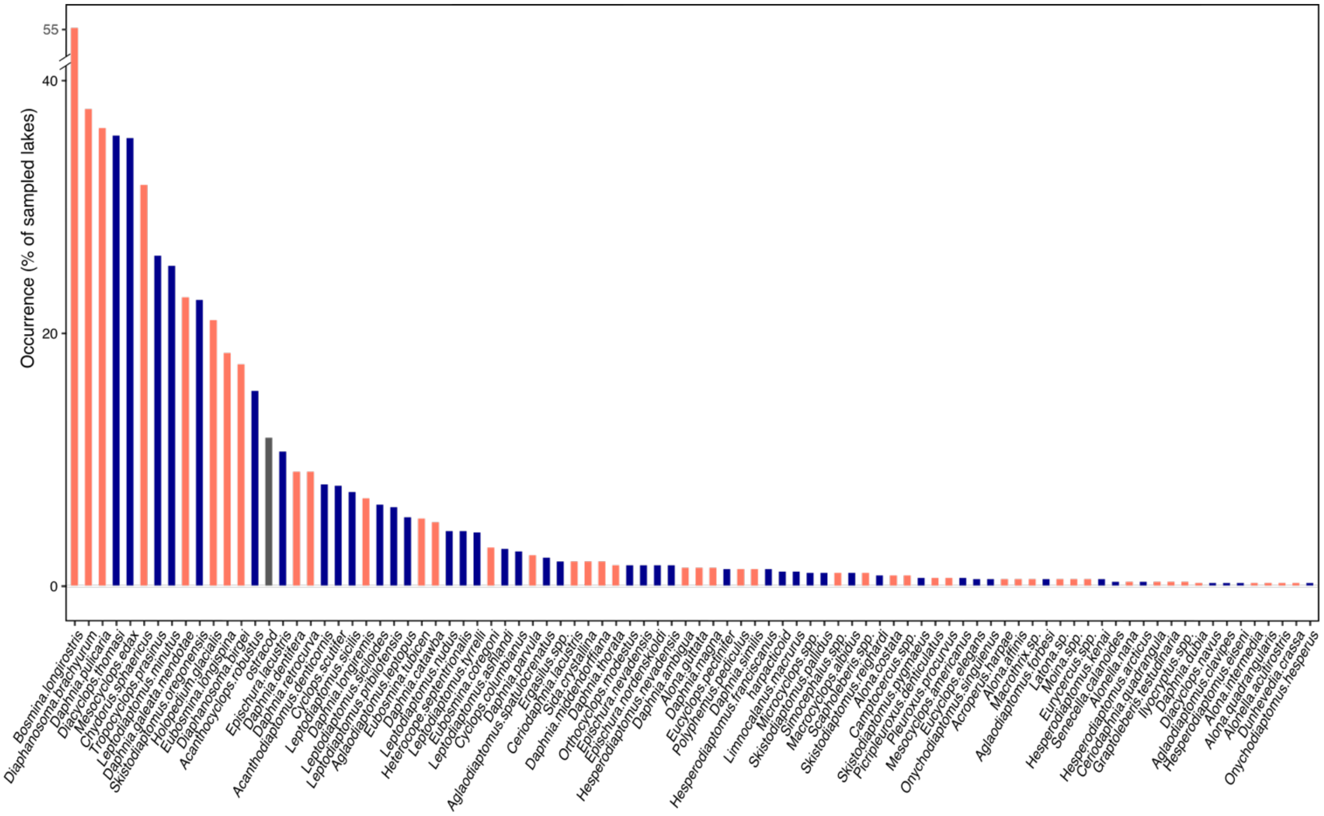


Figure F.1 Rank-frequency occurrences of the 90 pelagic crustacean taxa collected in 624 lakes across Canada. Orange bars represent cladoceran species and blue bars represent copepod species.

ANNEXE G

β-DIVERSITY

Table G.1 Total taxonomic β-diversity, replacement (turnover) and richness difference (rich diff; nestedness) components and local contributions to β-diversity (LCBD) values as computed with *beta.div()* and *beta.div.comp()* by ecozone (a) and continental divide (b). Significant *p*-values from the ANOVAs are shown. Largest index values are highlighted in bold.

(a) Ecozone	**β-diversity**	**Replacement / total**	**Rich diff/ total**	**LCBD**
All	0.47	0.37	0.63	0.0016
Boreal Cordillera	0.42	**0.50**	0.50	**0.0017**
Taiga Plains	**0.46**	0.35	0.65	**0.0017**
Pacific Maritime	0.45	0.34	0.66	0.0016
Montane Cordillera	0.42	0.43	0.57	0.0016
Semi-Arid Plateaux	0.42	0.38	0.62	0.0016
Boreal Plains	0.45	0.32	**0.68**	0.0016
Prairies	0.45	0.32	**0.68**	**0.0017**
Boreal Shield	0.44	0.47	0.53	0.0016
Mixedwood Plains	0.44	0.45	0.55	0.0016
Atlantic Highlands	0.44	0.43	0.57	0.0016
Atlantic Maritime	0.44	0.38	0.62	0.0016
p-value	-	-	-	<2e-16

(b) Continental basin	**β-diversity**	**Replacement / total**	**Rich diff/ total**	**LCBD**
All	0.47	0.37	0.63	0.0016
Pacific Ocean	0.45	0.38	0.62	0.0016
Arctic Ocean	**0.46**	0.36	0.64	**0.0017**
Hudson Bay	**0.46**	0.30	**0.70**	0.0016
Great Lakes-St. Lawrence	0.44	**0.46**	0.54	0.0016
Atlantic Ocean	0.43	0.37	0.63	0.0016
p-value	-	-	-	6.34e-06

Table G.2 Total functional β-diversity, replacement (turnover) and richness difference (rich diff; nestedness) components computed with *multidimFbetaD()* and local contribution to β-diversity (LCBD) values computed with *LCBD.comp()* by ecozone (a) and continental divide (b). Significant *p*-values from the ANOVAs are shown. Largest index values are highlighted in bold.

(a) Ecozone	**β-diversity**	**Replacement / total**	**Rich diff/ total**	**LCBD**
All	0.32	0.48	0.52	0.0016
Boreal Cordillera	**0.34**	0.52	0.48	**0.0022**
Taiga Plains	0.33	**0.58**	0.42	0.0018
Pacific Maritime	0.31	0.42	0.58	0.0017
Montane Cordillera	0.33	0.53	0.47	0.0018
Semi-Arid Plateaux	**0.34**	0.48	0.52	0.0019
Boreal Plains	0.27	0.36	**0.64**	0.0015
Prairies	0.31	0.47	0.53	0.0016
Boreal Shield	0.28	0.45	0.55	0.0015
Mixedwood Plains	0.25	0.36	**0.64**	0.0014
Atlantic Highlands	0.28	0.48	0.52	0.0015
Atlantic Maritime	0.30	0.40	0.60	0.0016
p-value	-	-	-	1.06e-08

(b) Continental basin	**β-diversity**	**Replacement / total**	**Rich diff/ total**	**LCBD**
All	0.32	0.48	0.52	0.0016
Pacific Ocean	**0.35**	0.52	0.48	**0.0018**
Arctic Ocean	0.33	**0.55**	0.45	0.0017
Hudson Bay	0.29	0.42	0.58	0.0017
Great Lakes-St. Lawrence	0.28	0.47	0.53	0.0015
Atlantic Ocean	0.31	0.38	**0.62**	0.0016
p-value	-	-	-	1.82e-06

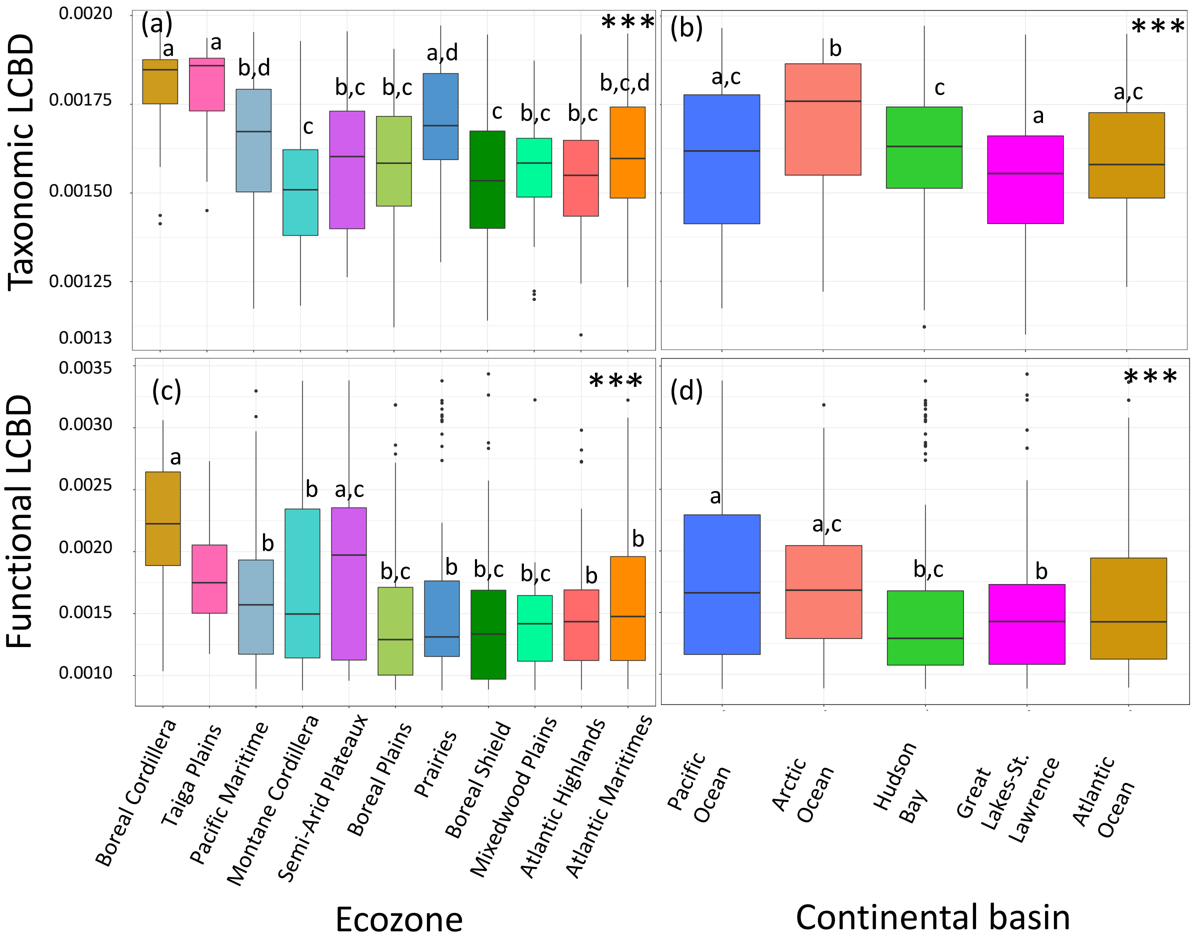


Figure G.1 Taxonomic (a,b) and functional (c,d) local contribution to β-diversity (LCBD) means (± SE across ecozones and continental basins respectively). Note that the y-axis scale varies between panels. Boxes that share the same letter are not significantly different. **p*-value<0.05; ***p*-value<0.01; ****p*-value<0.001.

Table G.3 Species with taxonomic (a) and functional (b) Species contribution to β-diversity (SCBD) larger than mean SCBD, as computed with *beta.div()* function.

(a) Species	**Taxonomic SCBD**
Daphnia pulicaria	0.15
Bosmina longirostris	0.07
Leptodiaptomus minutus	0.06
Skistodiaptomus oregonensis	0.06
Mesocyclops edax	0.06
Daphnia.galeata mendotae	0.05
Diacyclops thomasi	0.04
Leptodiaptomus sicilis	0.03
Holopedium glacialis	0.03
Leptodiaptomus pribilofensis	0.03
Daphnia dentifera	0.03
Tropocyclops prasinus	0.03
Acanthocyclops robustus	0.02
Daphnia catawba	0.02
Aglaodiaptomus leptopus	0.02
Daphnia retrocurva	0.02
Leptodiaptomus siciloides	0.02
Epischura lacustris	0.02
Acanthodiaptomus denticornis	0.02
Heterocope septentrionalis	0.02
Diaphanosoma brachyurum	0.02
Leptodiaptomus nudus	0.01
Cyclops columbianus	0.01
Diaphanosoma birgei	0.01
Cyclops scutifer	0.01
Eubosmina longispina	0.01
Chydorus sphaericus	0.01

(b) Species	**Functional SCBD**
Bosmina longirostris	0.019
Eubosmina tubicen	0.019
Aglaodiaptomus clavipes	0.018
Aglaodiaptomus forbesi	0.018
Aglaodiaptomus leptopus	0.018
Aglaodiaptomus spatulocrenatus	0.018
Eubosmina coregoni	0.018
Bosmina longispina	0.018
Heterocope septentrionalis	0.018
Macrocyclops albidus	0.018
Orthocyclops modestus	0.018
Skistodiaptomus pallidus	0.018
Acanthocyclops robustus	0.017
Polyphemus pediculus	0.017
Epischura nevadensis	0.016
Epischura nordenskioldi	0.016
Alona affinis	0.013
Alona costata	0.013
Alona guttata	0.013
Alona intermedia	0.013
Alona quadrangularis	0.013
Alonella acutirostris	0.013
Alonella nana	0.013
Camptocercus sp	0.013
Chydorus sphaericus	0.013
Dunhevedia crassa	0.013
Eurycercus spp	0.013
Graptoleberis testudinaria	0.013
Hesperodiaptomus eiseni	0.013
Picripleuroxus denticulatus	0.013
Pleuroxus procurvus	0.013
Scapholeberis spp	0.013
Acanthodiaptomus denticornis	0.012
Acroperus harpae	0.012
Cyclops columbianus	0.012
Daphnia dubia	0.012

Table G.3 Continued

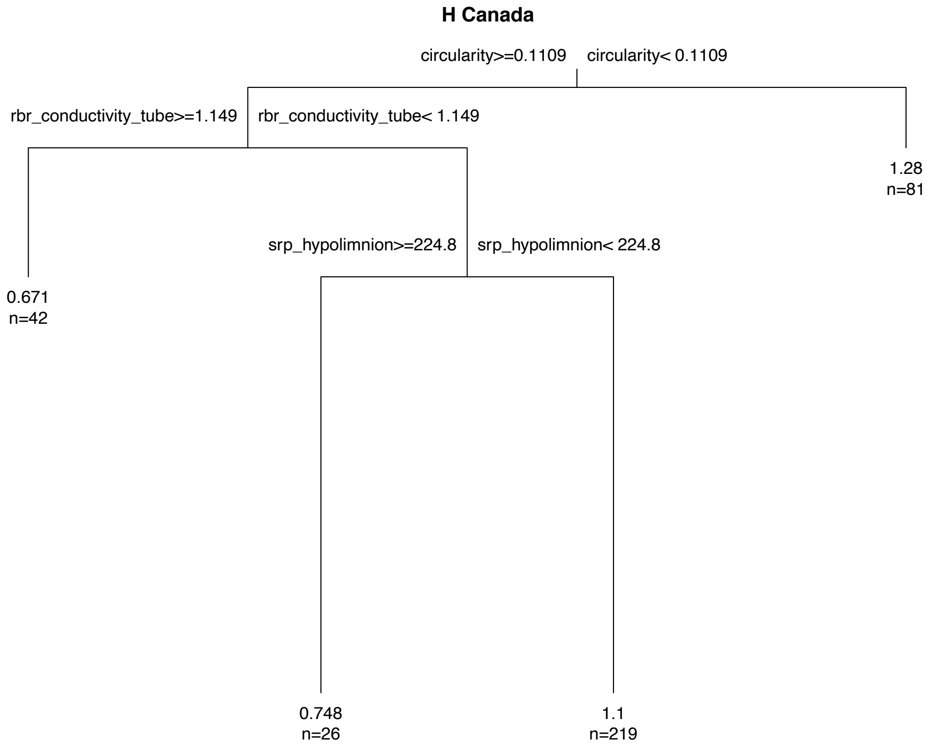
(b) Species	**Functional SCBD**
Daphnia pulicaria	0.012
Daphnia thorata	0.012
Diacyclops navus	0.012
Diacyclops thomasi	0.012
Hesperodiaptomus franciscanus	0.012
Hesperodiaptomus kenai	0.012
Hesperodiaptomus nevadensis	0.012
Leptodiaptomus sicilis	0.012
Limnocalanus macrurus	0.012
Mesocyclops edax	0.012
Skistodiaptomus oregonensis	0.012
Skistodiaptomus pygmaeus	0.012
Skistodiaptomus reighardi	0.012
Harpacticoida	0.011

ANNEXE H

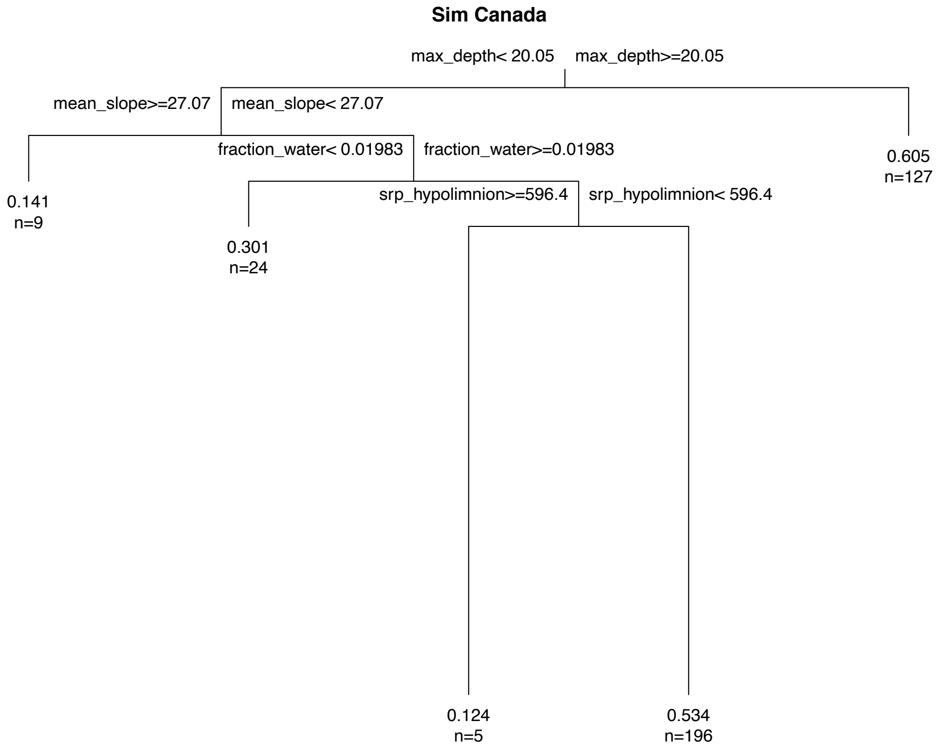
UNIVARIATE REGRESSION TREES (URTs)

Table H.1 Taxonomic and functional diversity indices URT errors , number of variables selected and first variable selected across Canada and by continental basin. Trees with the lowest cross-validated errors were selected. The smallest error values in each region are highlighted in bold.

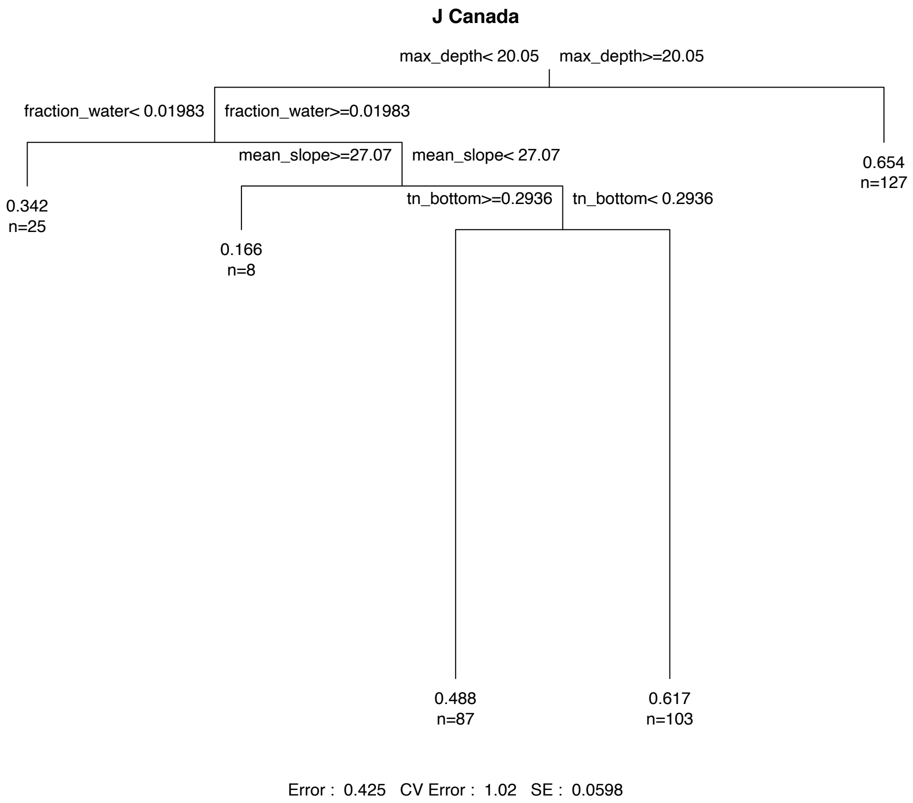
Diversity index	Canada	Pacific Ocean	Arctic Ocean	Hudson Bay	Great Lakes-St.Lawrence	Atlantic Ocean
Shannon	0.499 3 (circularity)	0.722 2 (T° watercolumn)	0.348 2 (pH epi)	0.793 1 (pH epi)	0.868 1 (depth)	0.692 1 (T° top meter)
Simpson	0.458 4 (depth)	0.879 1 (T° watercolumn)	0.621 2 (DOC)	0.858 1 (pH epi)	0.707 2 (depth)	0.675 1 (T° top meter)
Evenness	0.425 4 (depth)	0.645 3 (T° watercolumn)	0.741 1 (DOC)	0.695 2 (discharge)	0.593 3 (depth)	0.798 1 (water)
Richness	0.905 1 (circularity)	0.623 1 (DO tube)	0.22 2 (colour)	0.716 1 (pH epi)	0.783 1 (discharge)	0.797 1 (tn:tp ratio)
Rarefied Richness	0.815 2 (circularity)	0.793 1 (pH epi)	0.77 1 (T° watercolumn)	0.756 1 (forestry)	0.857 1 (circularity)	0.769 1 (depth)
Functional Evenness	0.73 3 (colour)	0.805 1 (conductivity hypo)	0.59 2 (pasture)	0.789 2 (sulfate)	0.813 1 (discharge)	0.863 1 (T° top meter)
Functional dispersion	0.442 2 (depth)	0.824 1 (T° watercolumn)	0.622 1 (water pressure_bottom)	0.871 1 (sulfate)	0.688 2 (depth)	0.619 1 (T° top meter)
Functional richness	0.776 4 (agriculture)	0.89 1 (urban)	0.618 1 (pH epi)	0.855 1 (SRP epi)	0.83 1 (chloride)	0.13 4 (chloride)

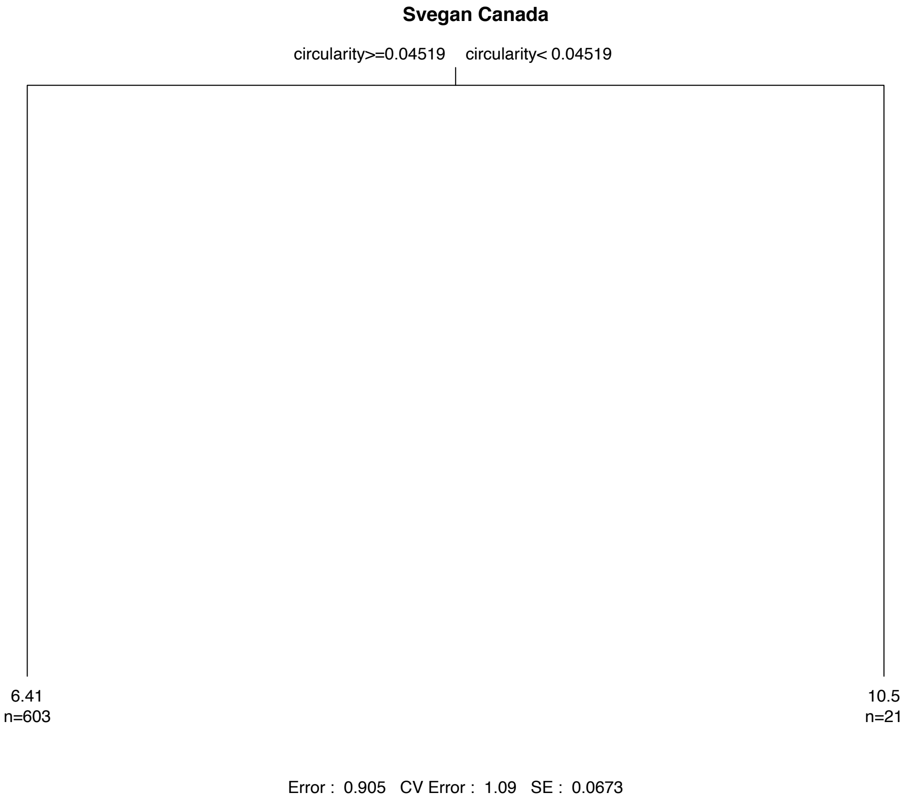


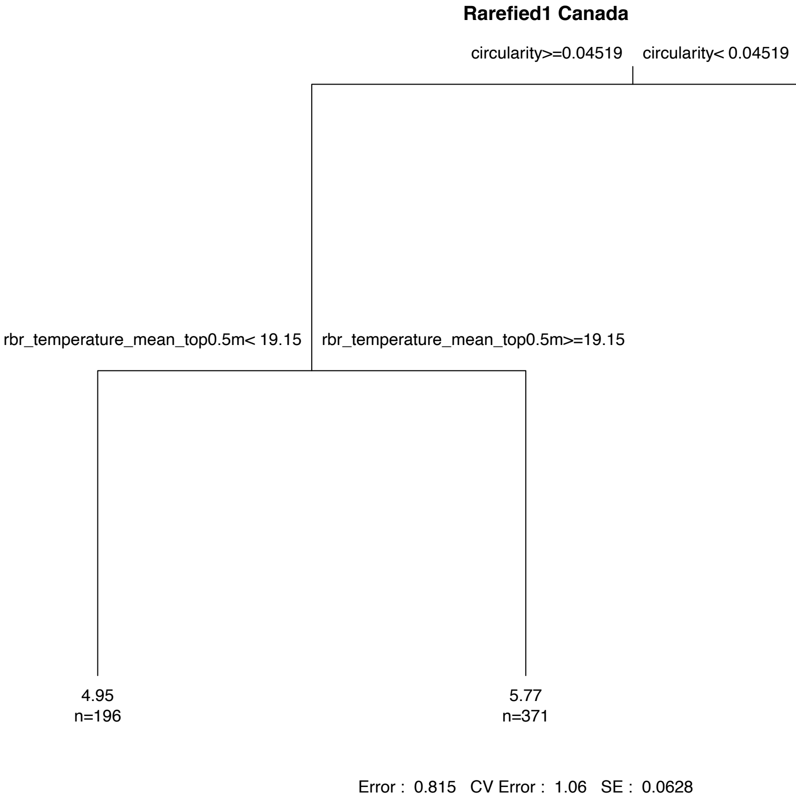
Error : 0.499 CV Error : 1.08 SE : 0.0551

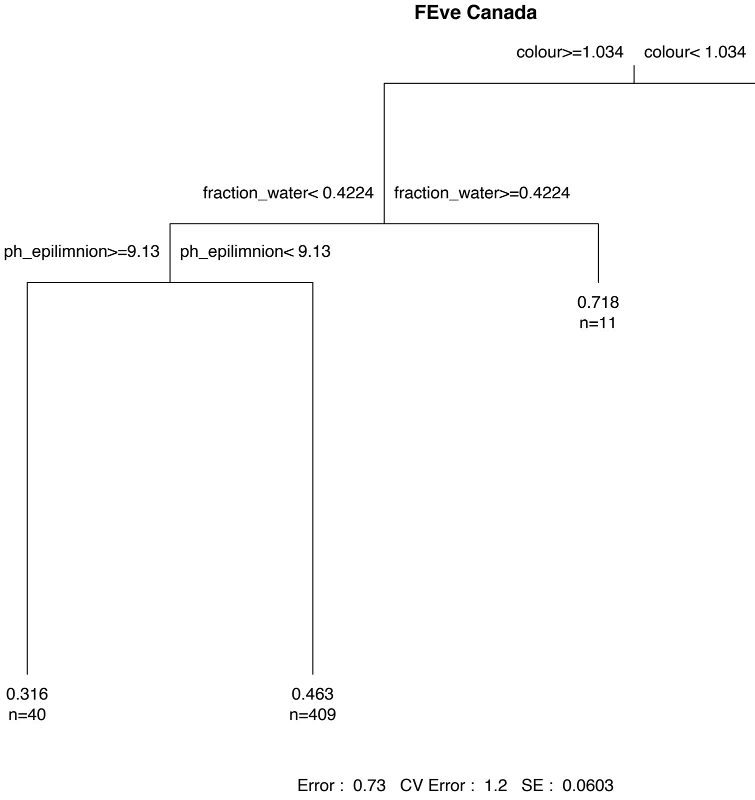


Error : 0.458 CV Error : 1.09 SE : 0.0613

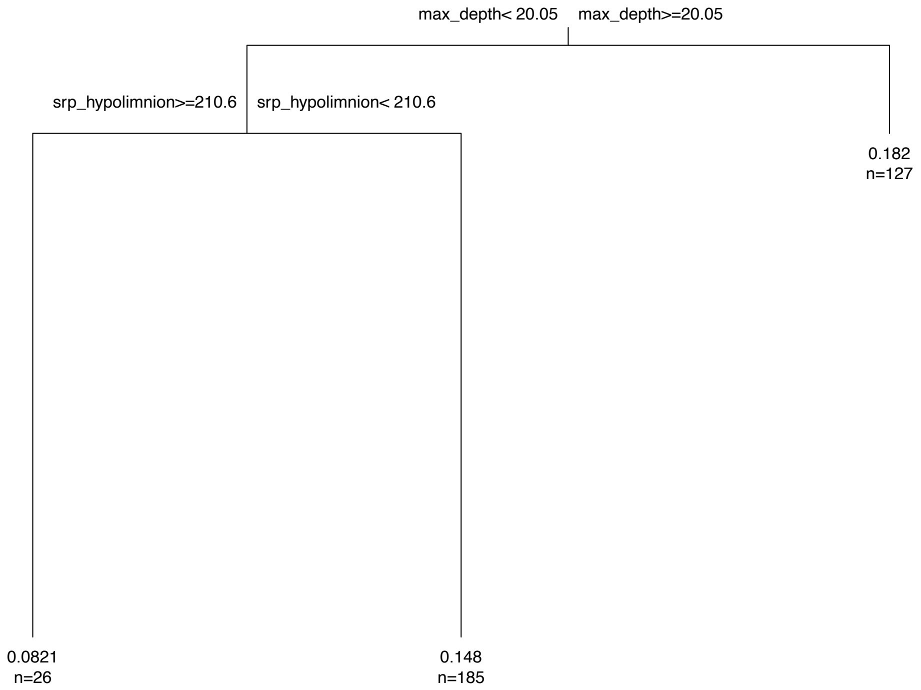

J Canada
max_depth< 20.05
max_depth>=20.05
fraction_water< 0.01983
fraction_water>=0.01983
mean_slope>=27.07
mean_slope< 27.07
tn_bottom>=0.2936
tn_bottom< 0.2936
0.342
n=25
0.166
n=8
0.488
n=87
0.617
n=103
0.654
n=127
Error : 0.425 CV Error : 1.02 SE : 0.0598


Svegan Canada
circularity>=0.04519
circularity< 0.04519
6.41
n=603
10.5
n=21
Error : 0.905 CV Error : 1.09 SE : 0.0673


Rarefied1 Canada
circularity>=0.04519
circularity< 0.04519
rbr_temperature_mean_top0.5m< 19.15
rbr_temperature_mean_top0.5m>=19.15
8.76
n=21
4.95
n=196
5.77
n=371
Error : 0.815 CV Error : 1.06 SE : 0.0628

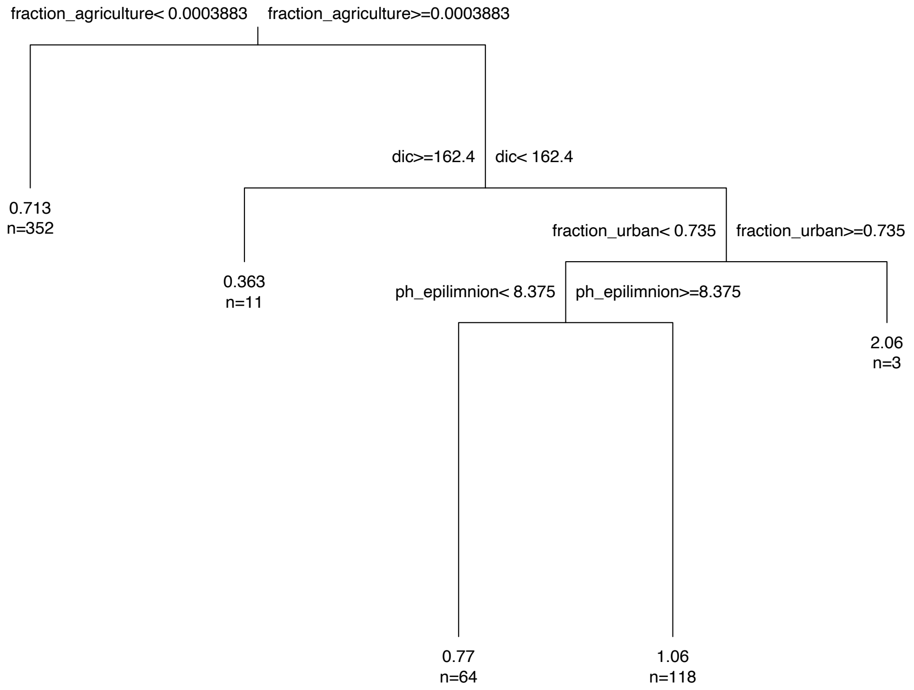

FEve Canada
colour>=1.034
colour< 1.034
fraction_water< 0.4224
fraction_water>=0.4224
ph_epilimnion>=9.13
ph_epilimnion< 9.13
0.679
n=16
0.718
n=11
0.316
n=40
0.463
n=409
Error : 0.73 CV Error : 1.2 SE : 0.0603

FDis Canada

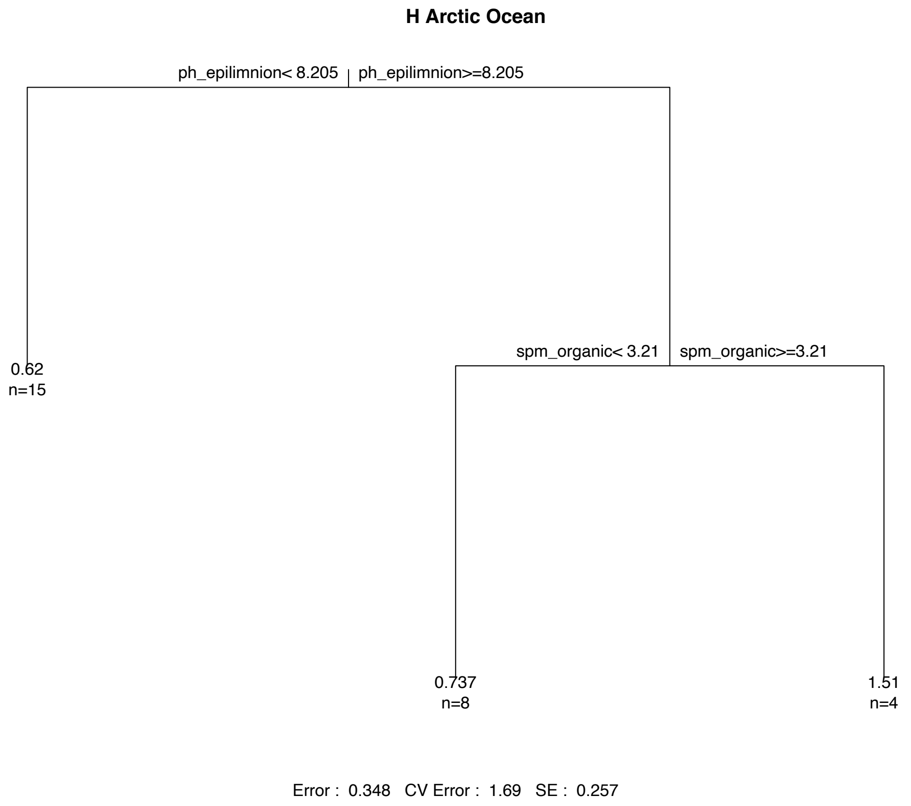


Error : 0.442 CV Error : 0.964 SE : 0.0515

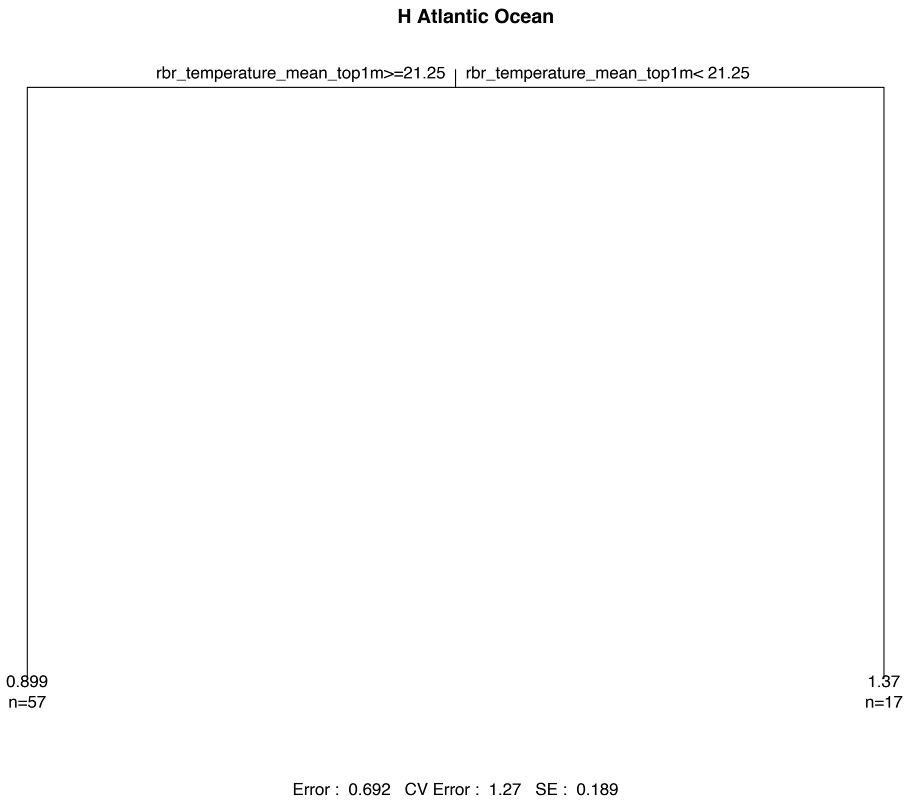
FRic Canada



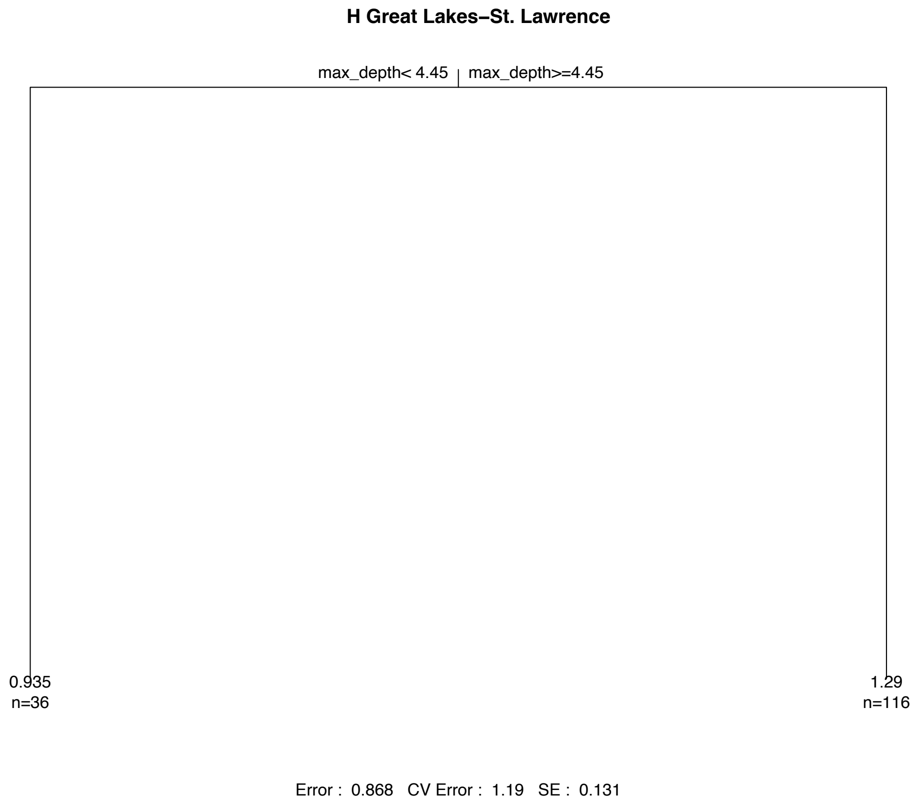
Error : 0.776 CV Error : 1.05 SE : 0.0587

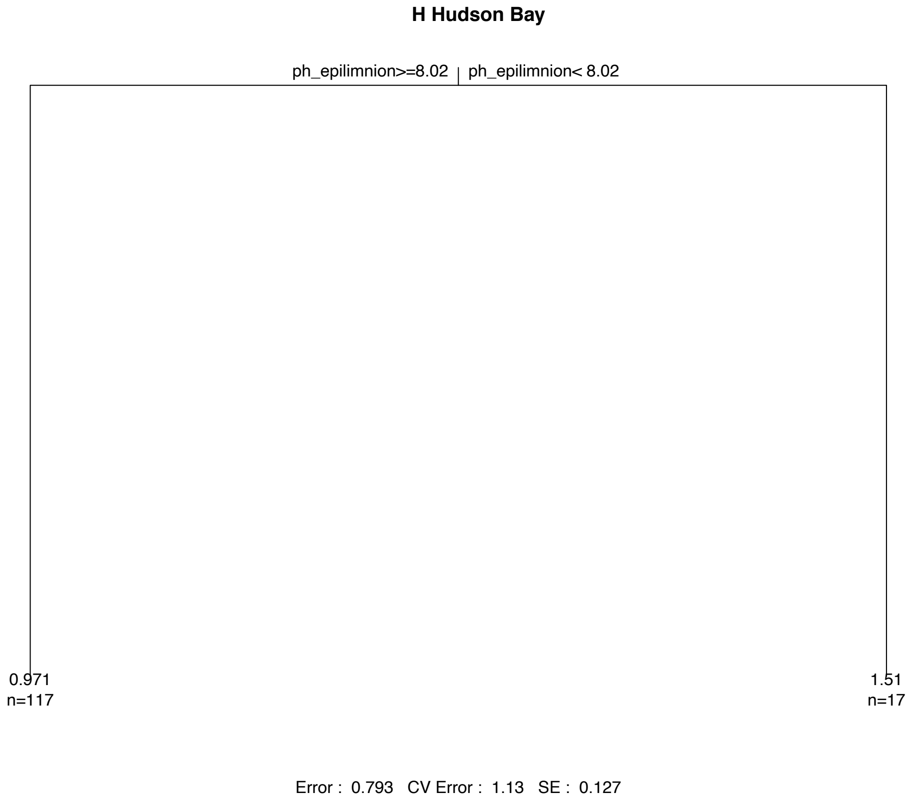

H Arctic Ocean

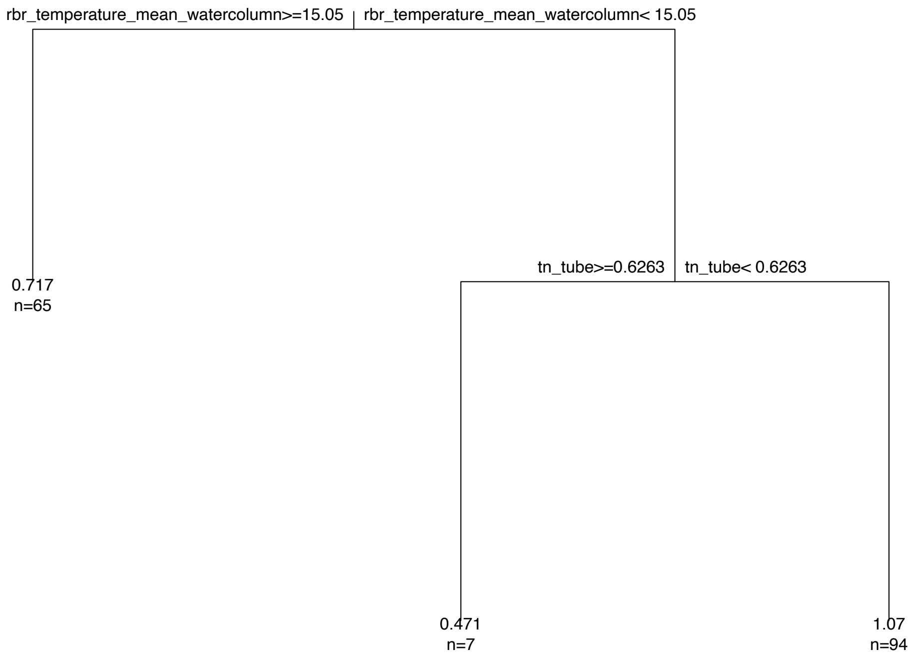
Error : 0.348   CV Error : 1.69   SE : 0.257


H Atlantic Ocean

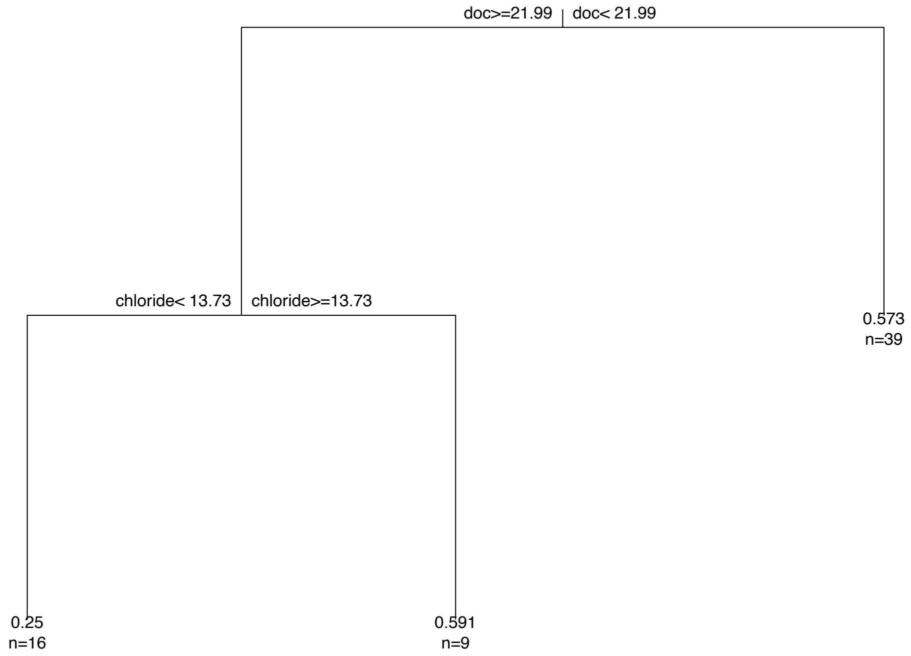
Error : 0.692   CV Error : 1.27   SE : 0.189


H Great Lakes–St. Lawrence
max_depth< 4.45
max_depth>=4.45
0.935
n=36
1.29
n=116
Error : 0.868   CV Error : 1.19   SE : 0.131

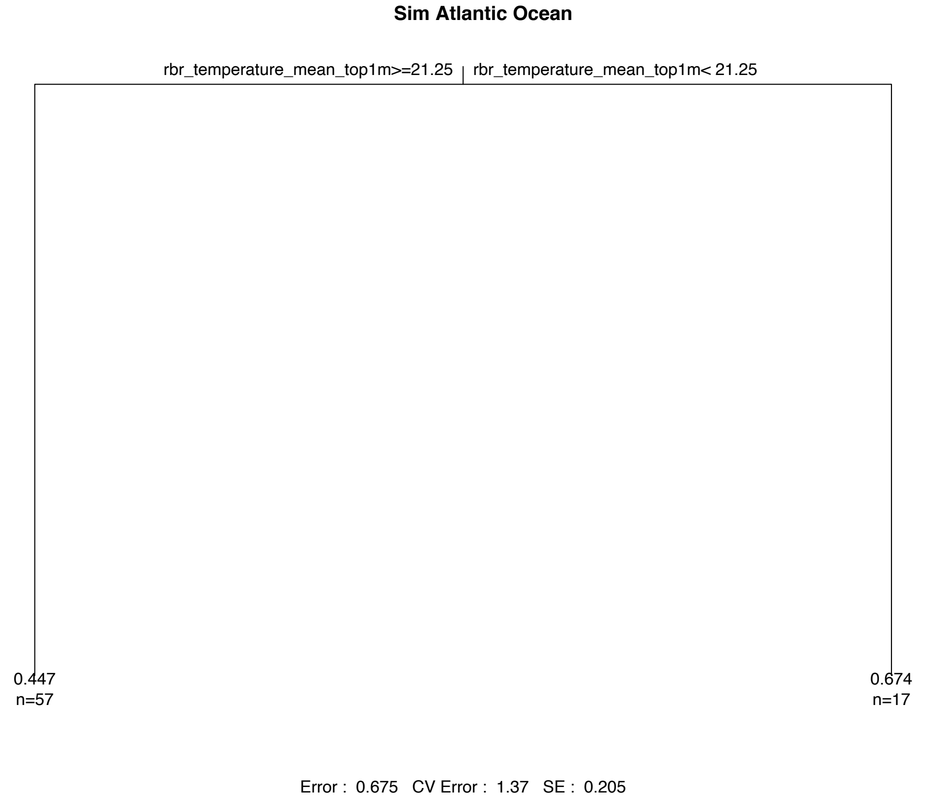

H Hudson Bay
ph_epilimnion>=8.02
ph_epilimnion< 8.02
0.971
n=117
1.51
n=17
Error : 0.793   CV Error : 1.13   SE : 0.127

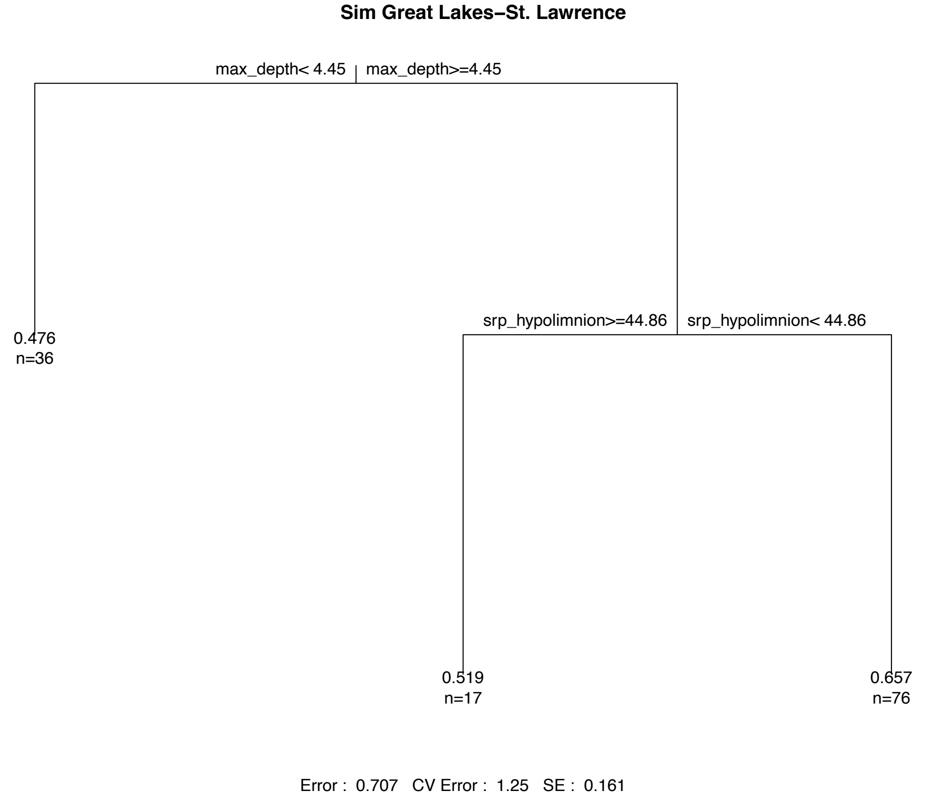

H Pacific Ocean

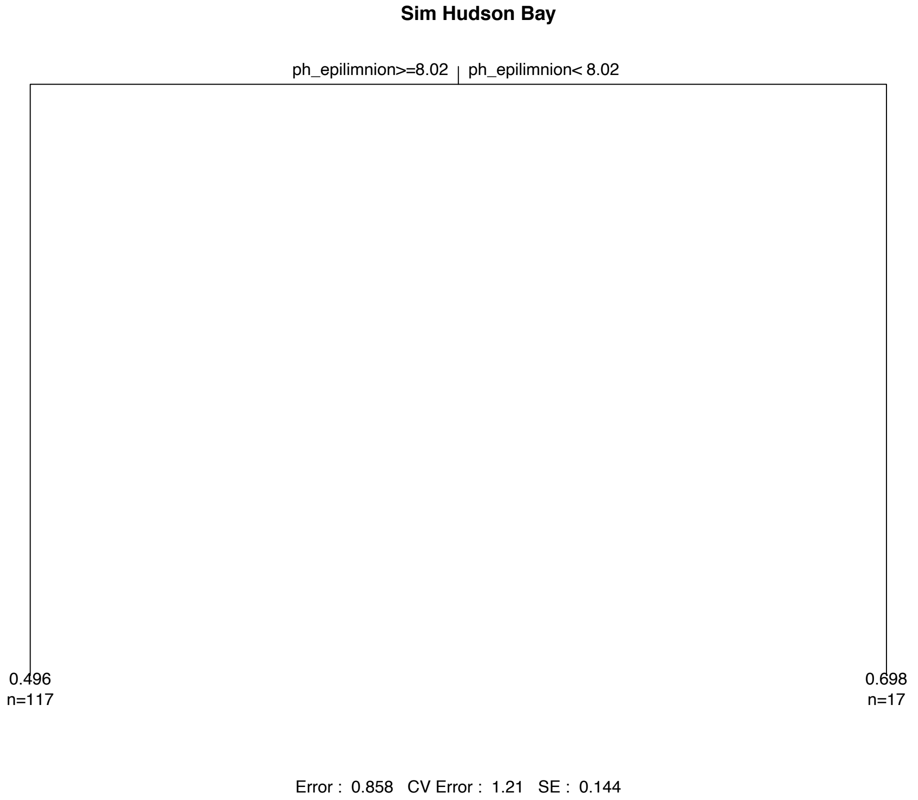
Error : 0.722 CV Error : 1.13 SE : 0.106

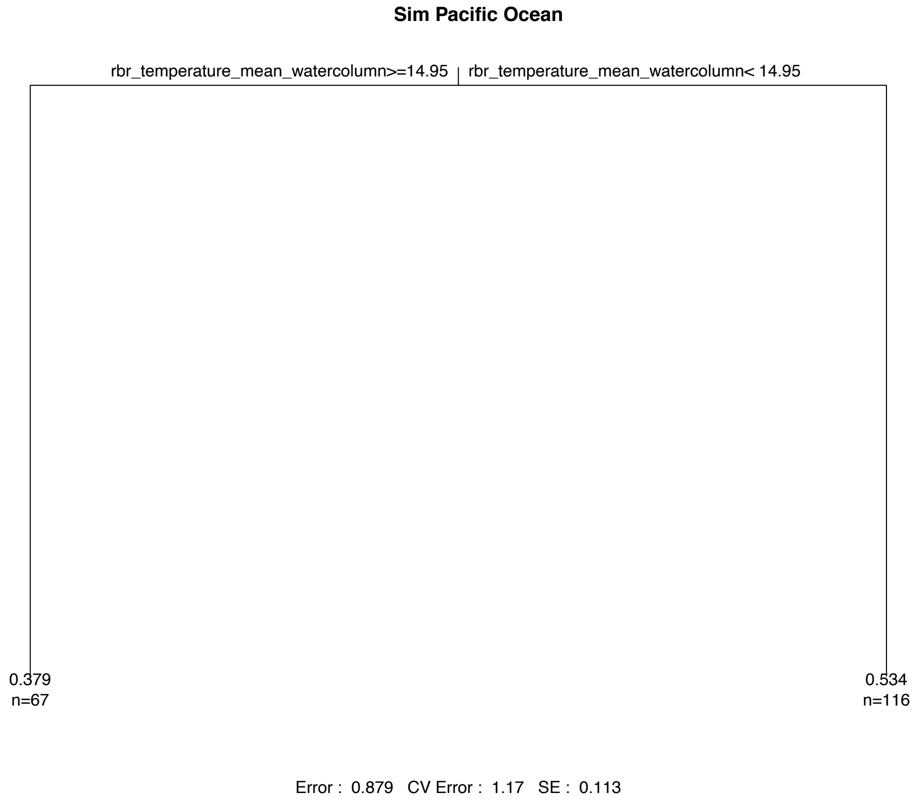

Sim Arctic Ocean

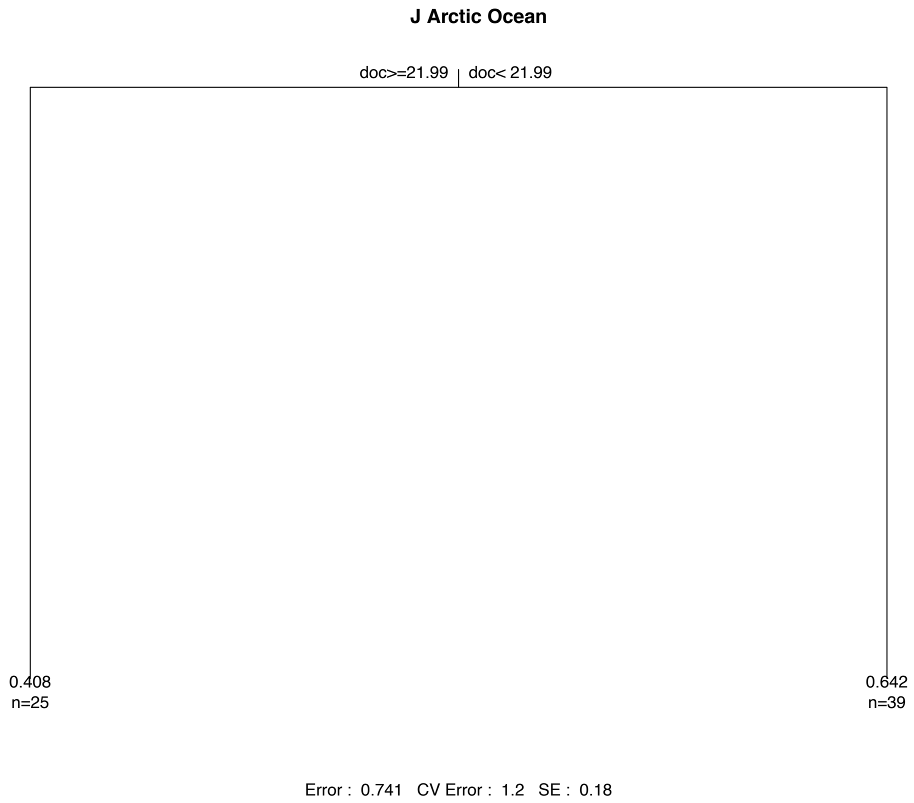
Error : 0.621 CV Error : 1.46 SE : 0.229

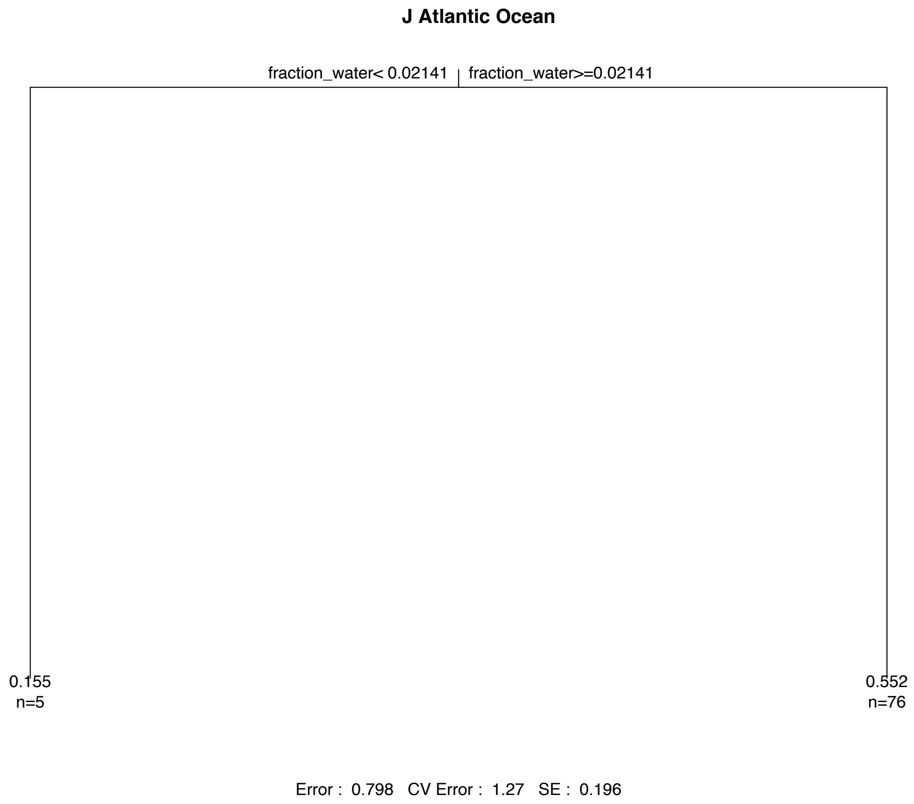

Sim Atlantic Ocean
rbr_temperature_mean_top1m>=21.25
rbr_temperature_mean_top1m< 21.25
0.447
n=57
0.674
n=17
Error : 0.675   CV Error : 1.37   SE : 0.205

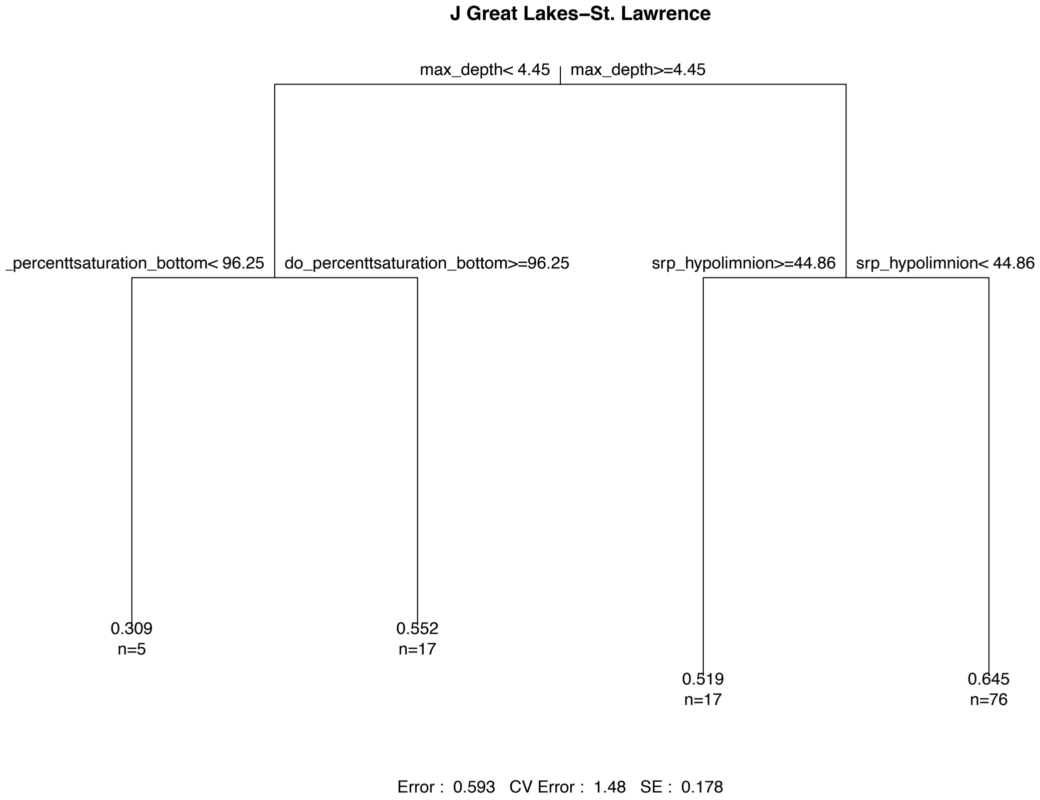

Sim Great Lakes–St. Lawrence
max_depth< 4.45
max_depth>=4.45
0.476
n=36
srp_hypolimnion>=44.86
srp_hypolimnion< 44.86
0.519
n=17
0.657
n=76
Error : 0.707   CV Error : 1.25   SE : 0.161

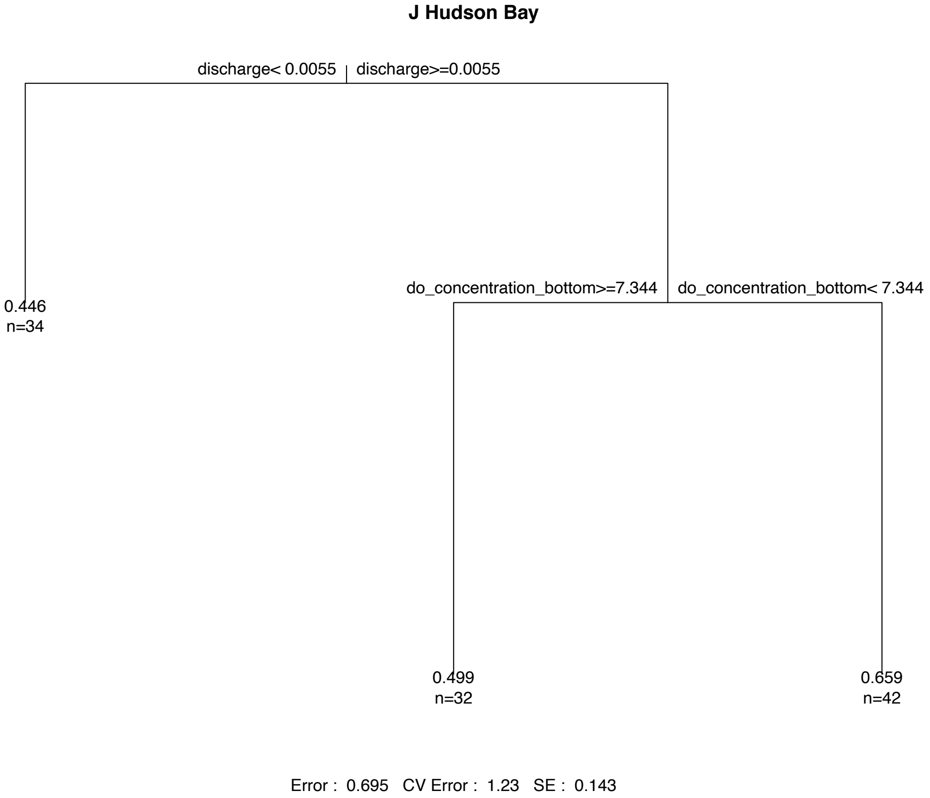

Sim Hudson Bay
ph_epilimnion>=8.02
ph_epilimnion< 8.02
0.496
n=117
0.698
n=17
Error : 0.858   CV Error : 1.21   SE : 0.144


Sim Pacific Ocean
rbr_temperature_mean_watercolumn>=14.95
rbr_temperature_mean_watercolumn< 14.95
0.379
n=67
0.534
n=116
Error : 0.879   CV Error : 1.17   SE : 0.113

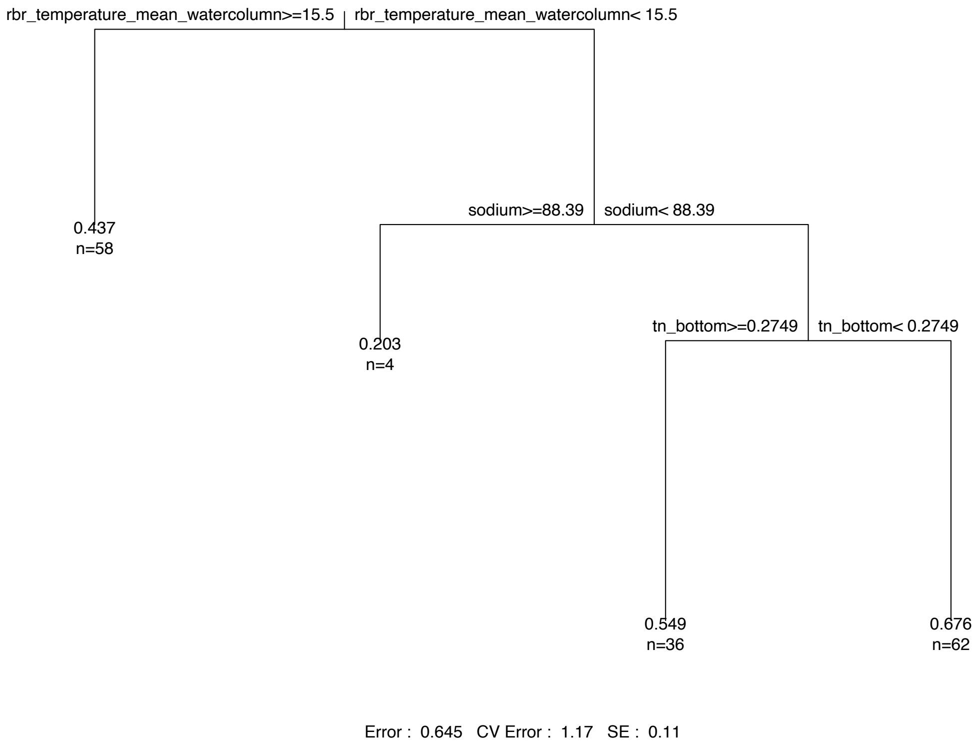

J Arctic Ocean
doc>=21.99
doc< 21.99
0.408
n=25
0.642
n=39
Error : 0.741   CV Error : 1.2   SE : 0.18


J Atlantic Ocean
fraction_water< 0.02141
fraction_water>=0.02141
0.155
n=5
0.552
n=76
Error : 0.798   CV Error : 1.27   SE : 0.196

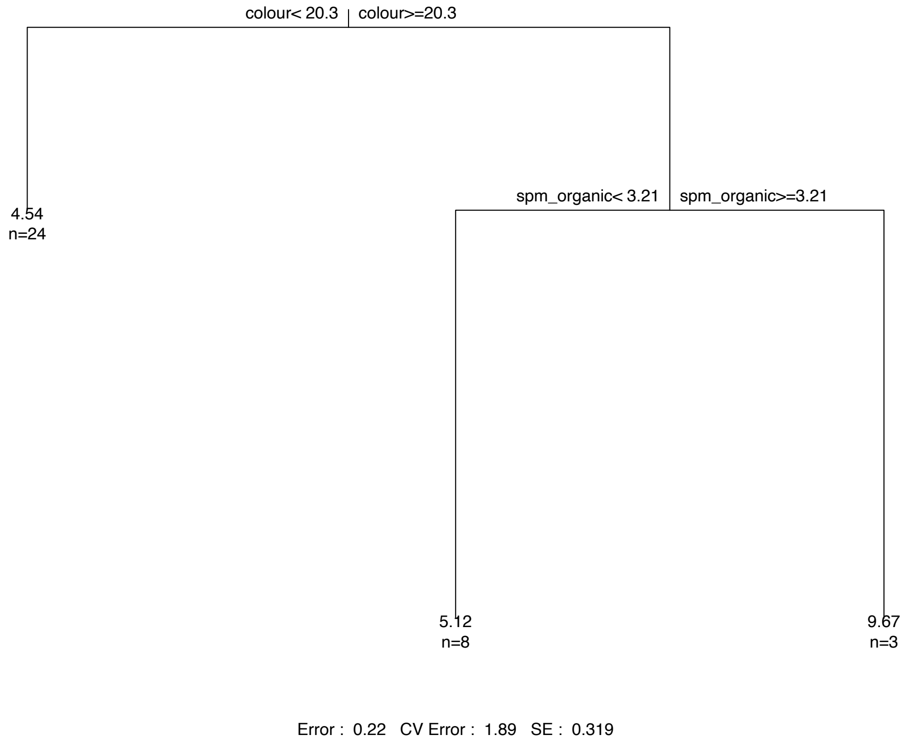

J Great Lakes–St. Lawrence
max_depth< 4.45
max_depth>=4.45
_percenttsaturation_bottom< 96.25
do_percenttsaturation_bottom>=96.25
srp_hypolimnion>=44.86
srp_hypolimnion< 44.86
0.309
n=5
0.552
n=17
0.519
n=17
0.645
n=76
Error : 0.593 CV Error : 1.48 SE : 0.178

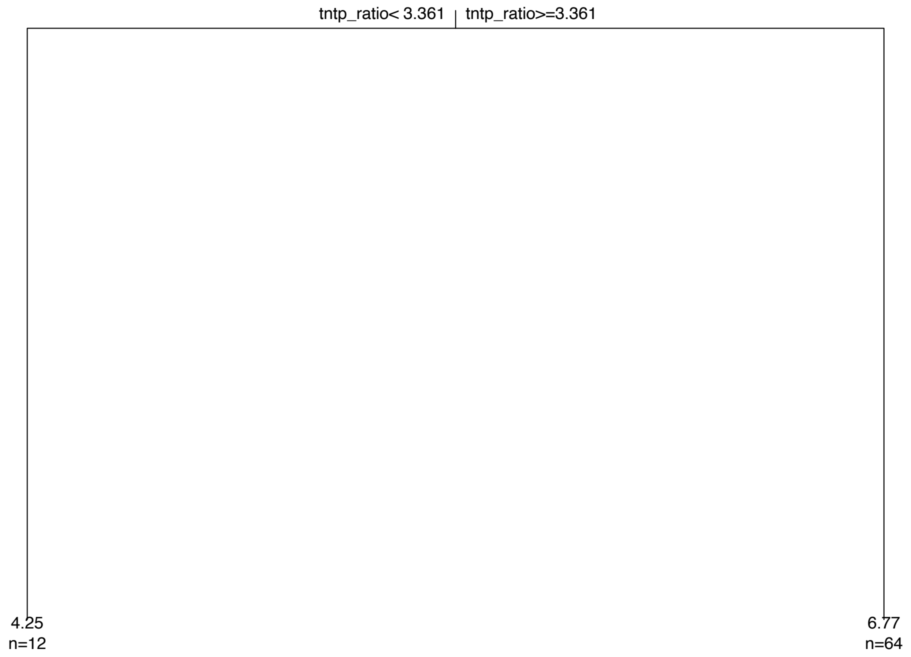

J Hudson Bay
discharge< 0.0055
discharge>=0.0055
0.446
n=34
do_concentration_bottom>=7.344
do_concentration_bottom< 7.344
0.499
n=32
0.659
n=42
Error : 0.695 CV Error : 1.23 SE : 0.143

J Pacific Ocean

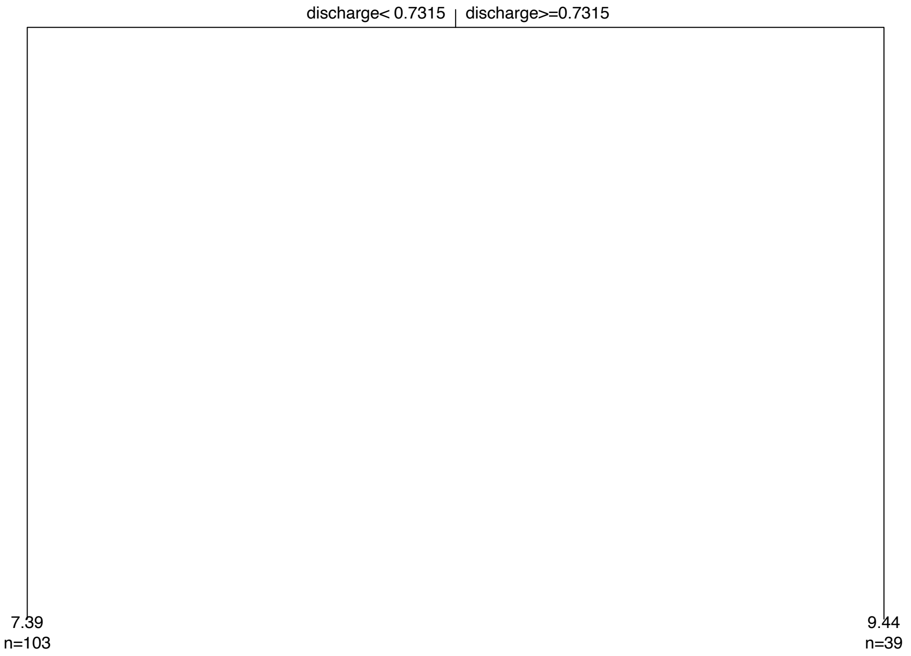


Svegan Arctic Ocean

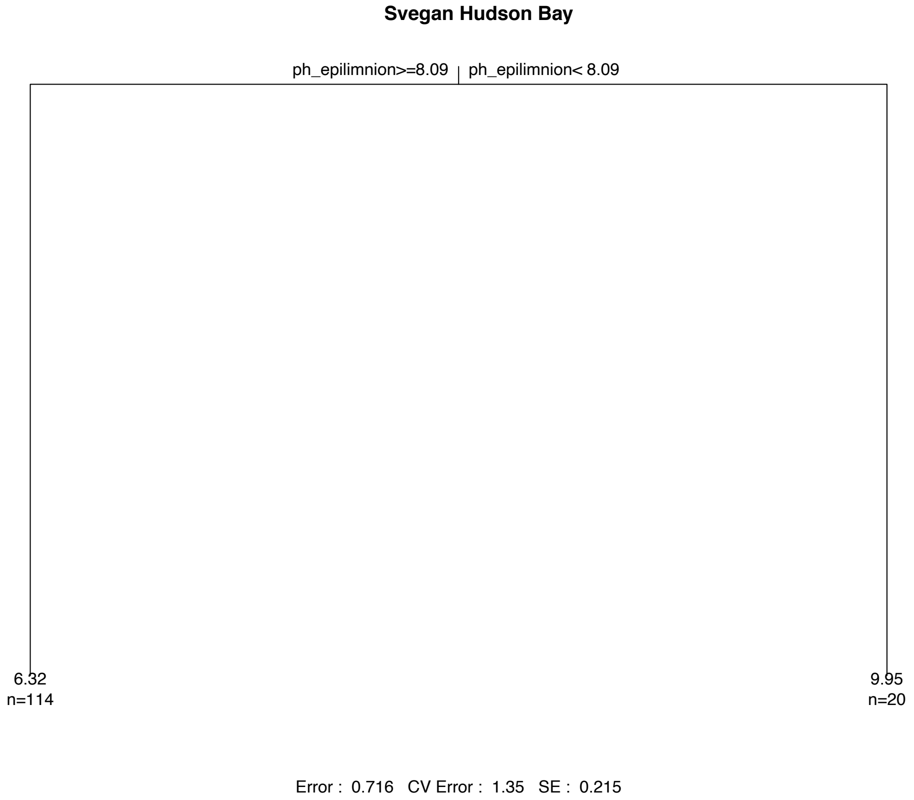


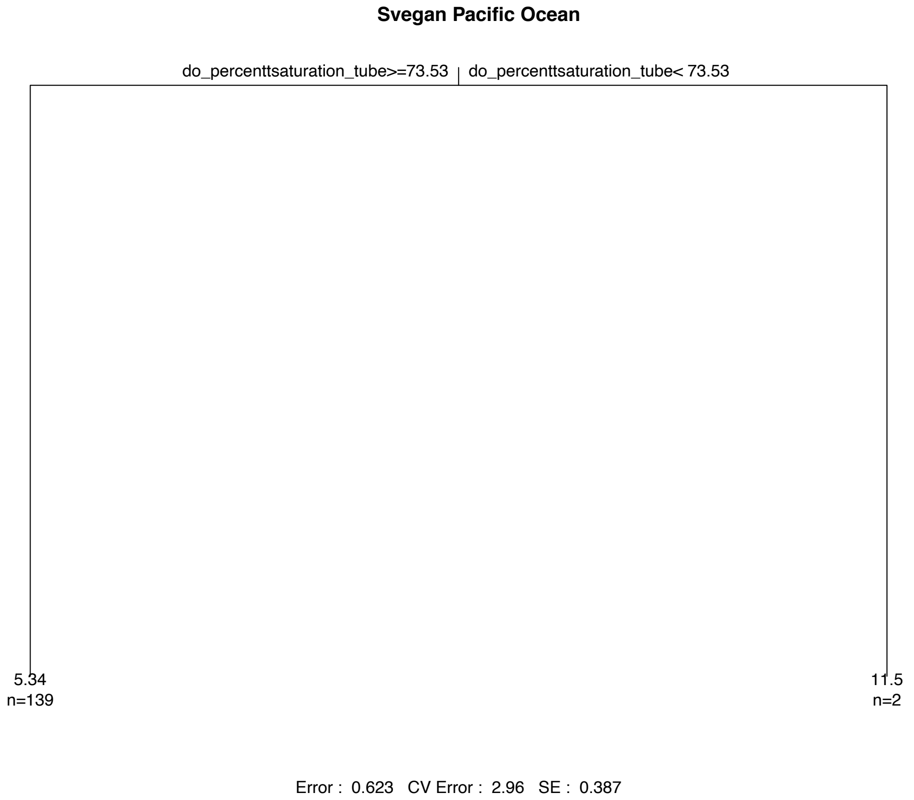

Svegan Atlantic Ocean

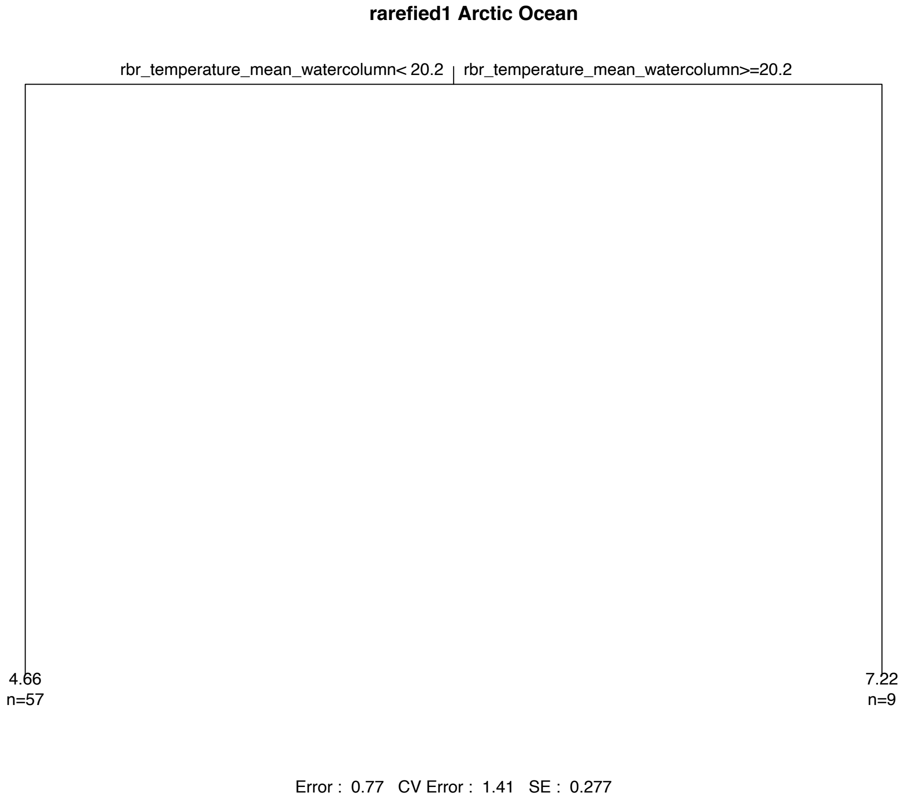
Error : 0.797 CV Error : 1.26 SE : 0.178

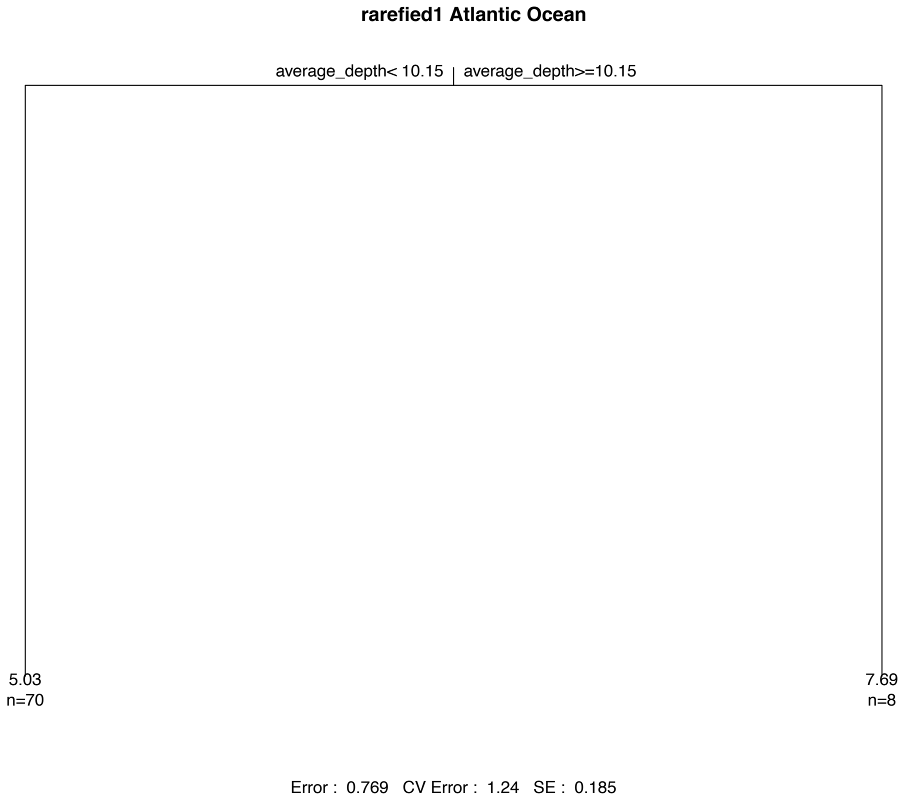

Svegan Great Lakes–St. Lawrence

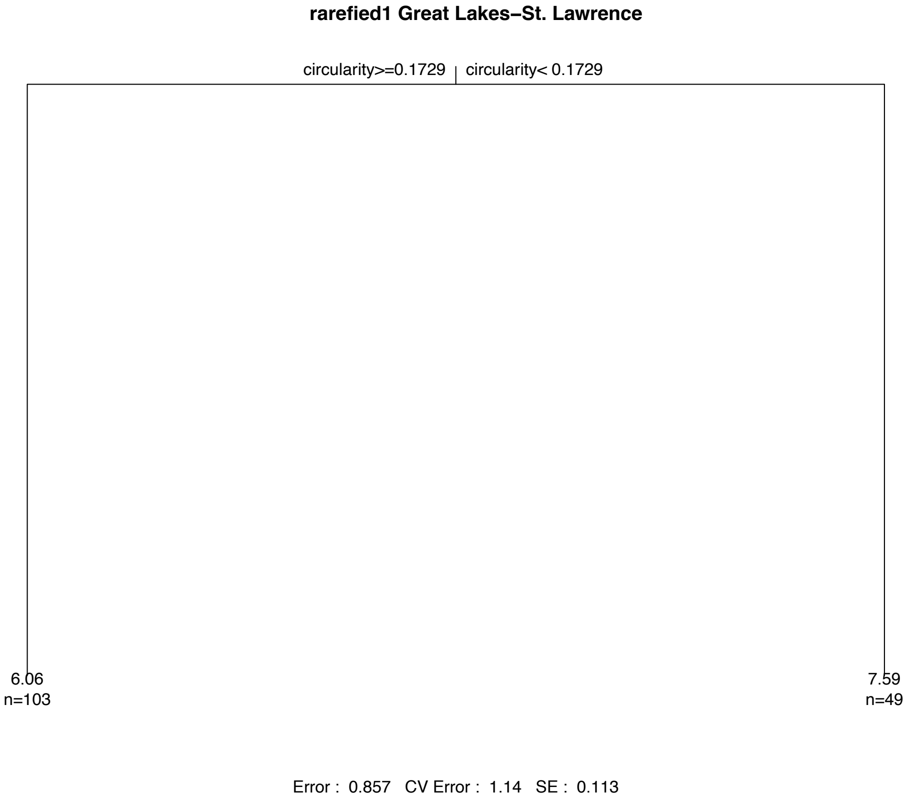
Error : 0.783 CV Error : 1.09 SE : 0.107

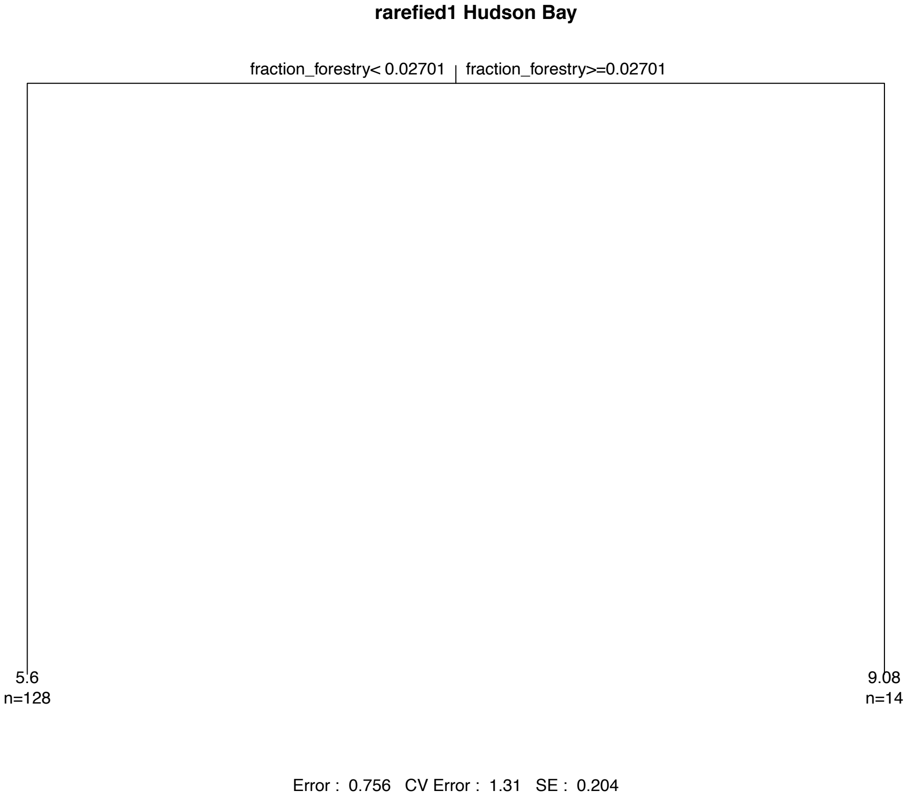

Svegan Hudson Bay
ph_epilimnion>=8.09
ph_epilimnion< 8.09
6.32
n=114
9.95
n=20
Error : 0.716 CV Error : 1.35 SE : 0.215

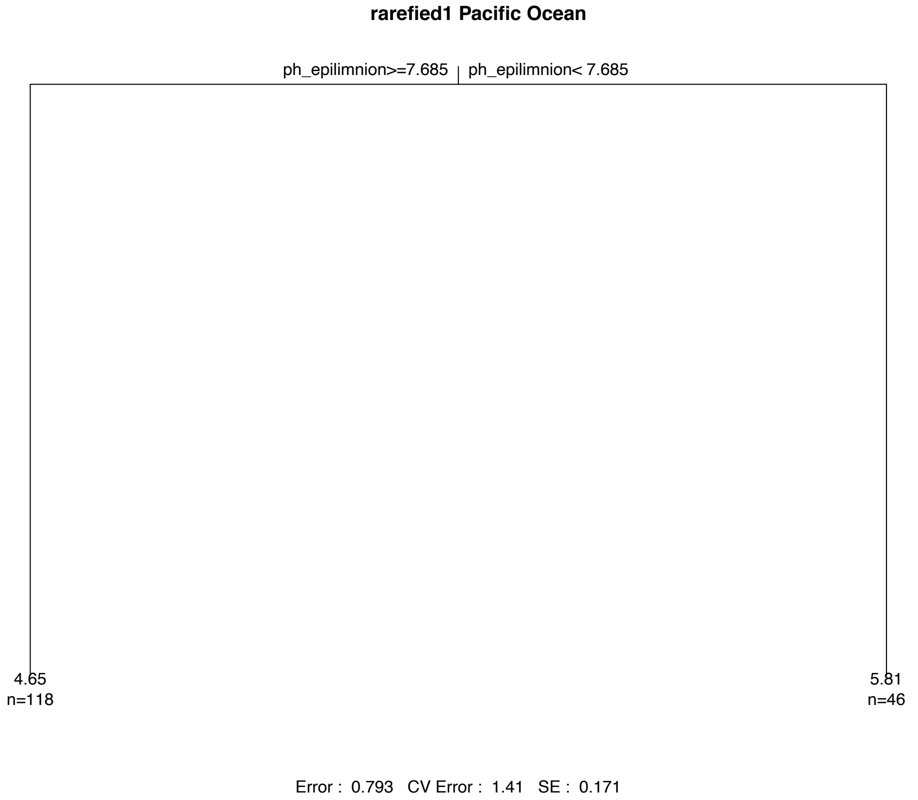

Svegan Pacific Ocean
do_percenttsaturation_tube>=73.53
do_percenttsaturation_tube< 73.53
5.34
n=139
11.5
n=2
Error : 0.623 CV Error : 2.96 SE : 0.387

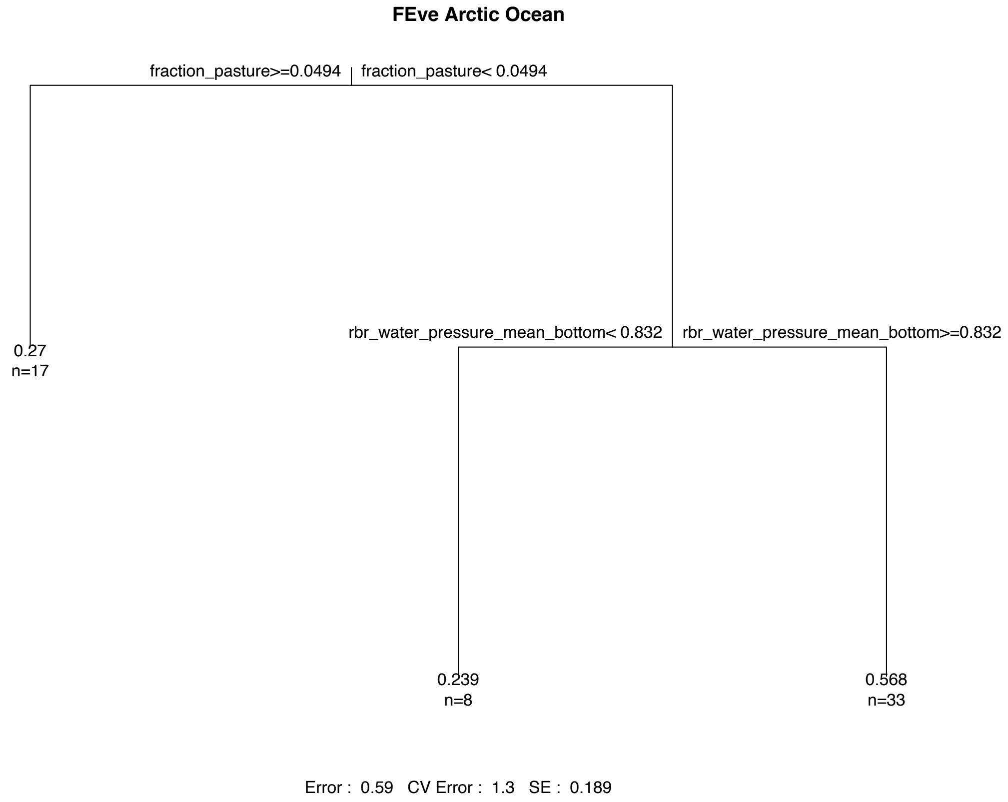

rarefied1 Arctic Ocean
rbr_temperature_mean_watercolumn< 20.2
rbr_temperature_mean_watercolumn>=20.2
4.66
n=57
7.22
n=9
Error : 0.77   CV Error : 1.41   SE : 0.277

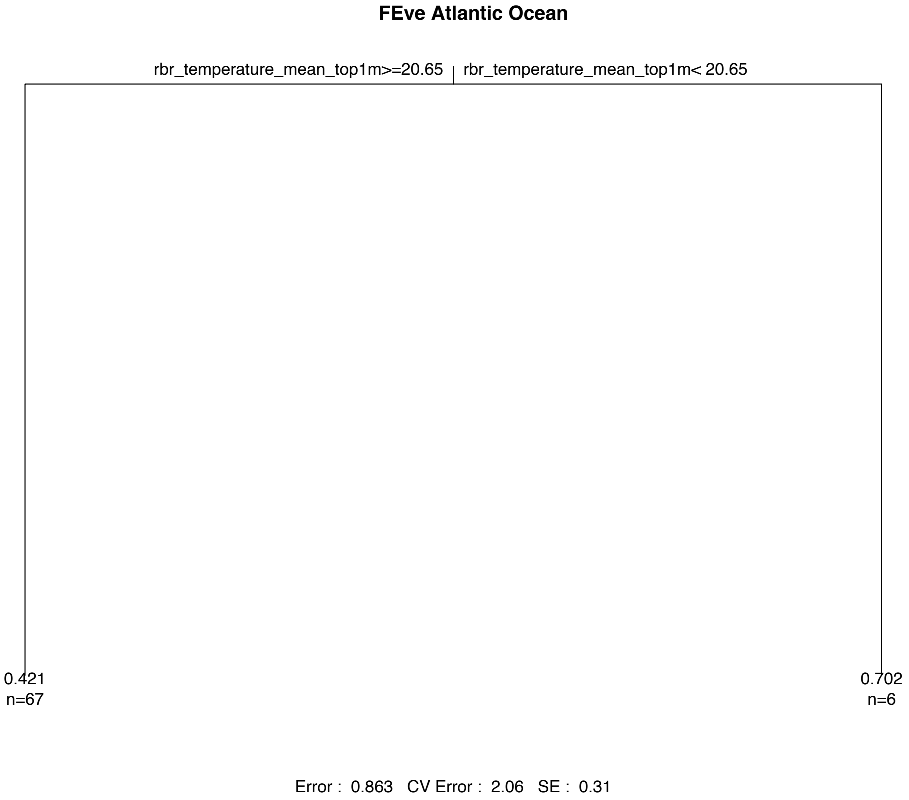

rarefied1 Atlantic Ocean
average_depth< 10.15
average_depth>=10.15
5.03
n=70
7.69
n=8
Error : 0.769   CV Error : 1.24   SE : 0.185

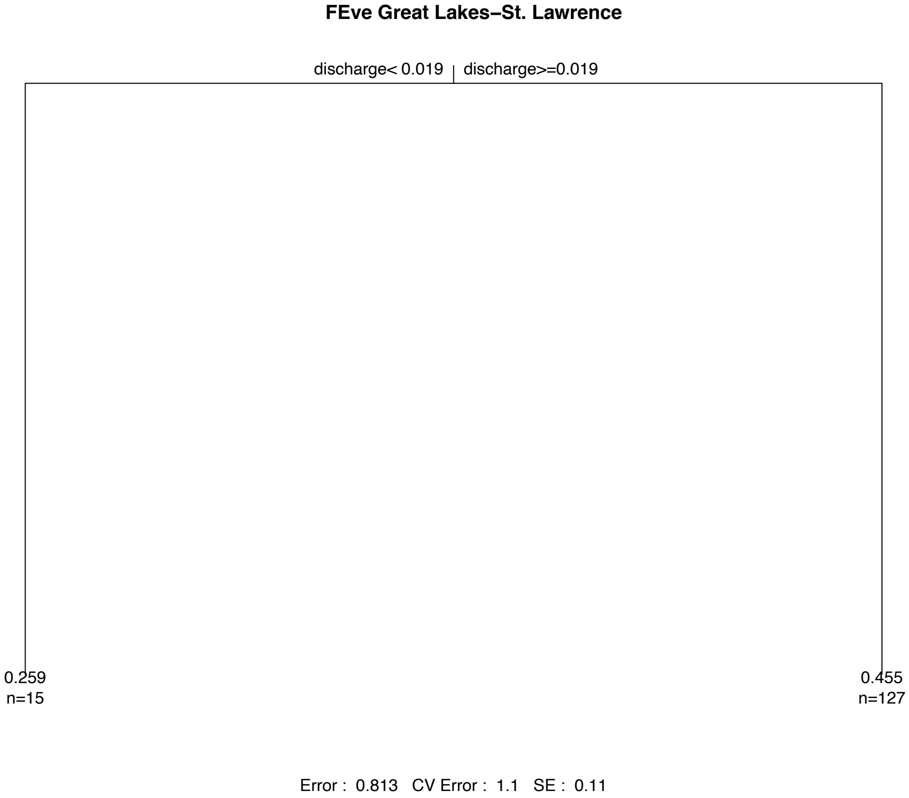

rarefied1 Great Lakes–St. Lawrence
circularity>=0.1729
circularity< 0.1729
6.06
n=103
7.59
n=49
Error : 0.857 CV Error : 1.14 SE : 0.113


rarefied1 Hudson Bay
fraction_forestry< 0.02701
fraction_forestry>=0.02701
5.6
n=128
9.08
n=14
Error : 0.756 CV Error : 1.31 SE : 0.204

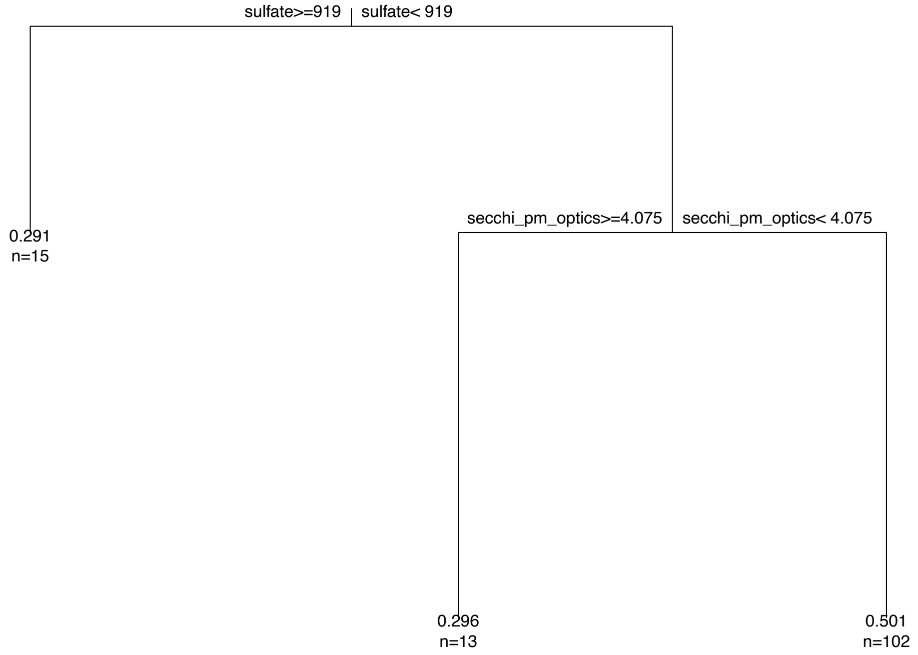

rarefied1 Pacific Ocean


FEve Arctic Ocean


FEve Atlantic Ocean
rbr_temperature_mean_top1m>=20.65
rbr_temperature_mean_top1m< 20.65
0.421
n=67
0.702
n=6
Error : 0.863   CV Error : 2.06   SE : 0.31


FEve Great Lakes–St. Lawrence
discharge< 0.019
discharge>=0.019
0.259
n=15
0.455
n=127
Error : 0.813   CV Error : 1.1   SE : 0.11

FEve Hudson Bay



Error : 0.789   CV Error : 1.28   SE : 0.132

FEve Pacific Ocean

Error : 0.805   CV Error : 1.08   SE : 0.0902

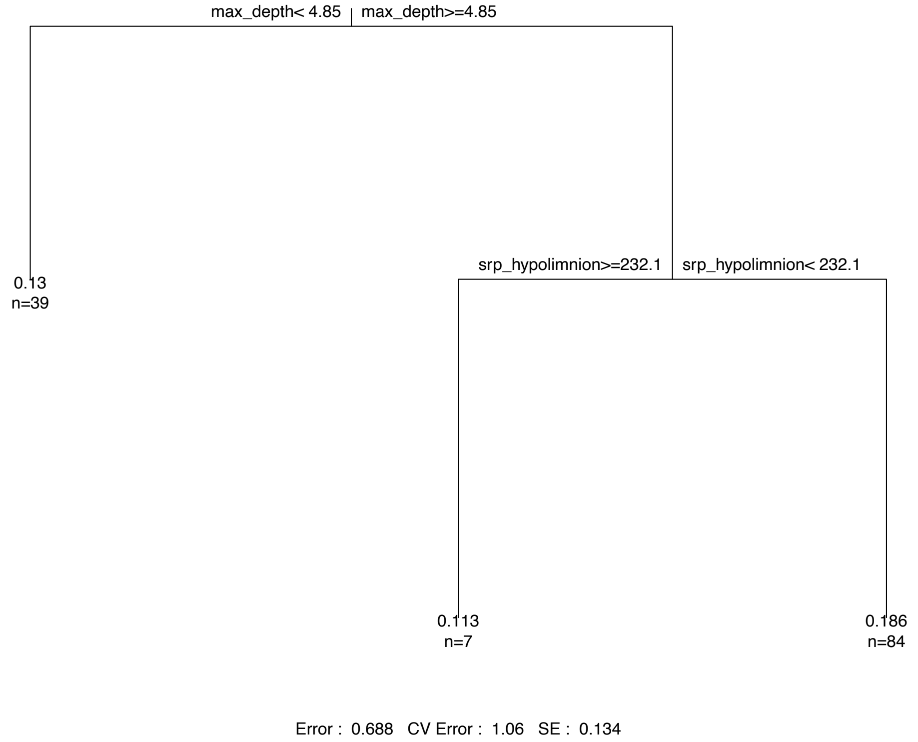
FDis Arctic Ocean

Error : 0.622 CV Error : 1.3 SE : 0.19

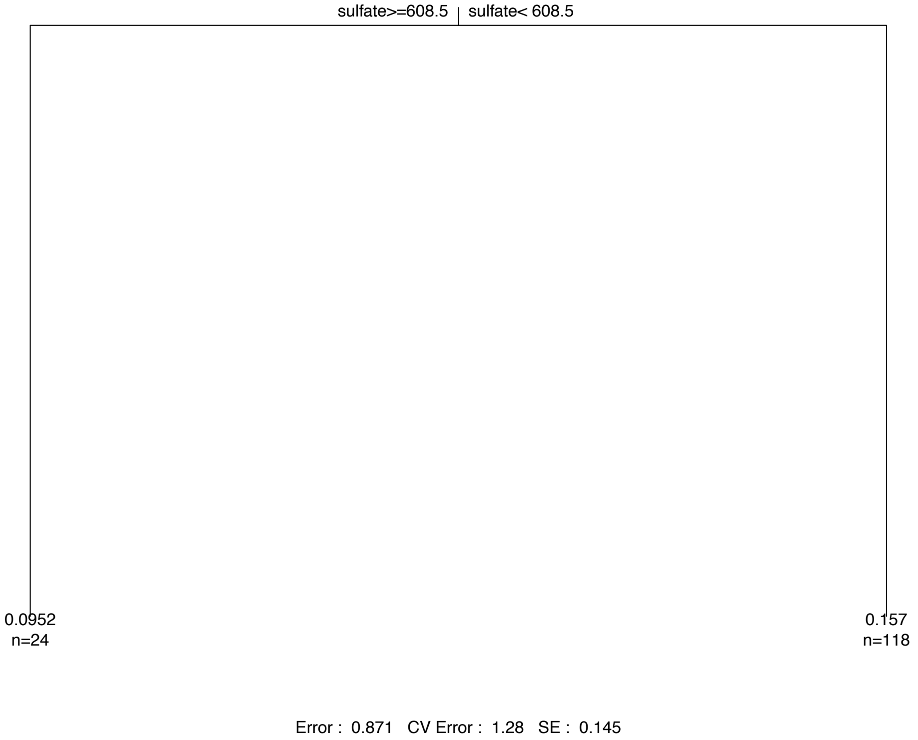
FDis Atlantic Ocean

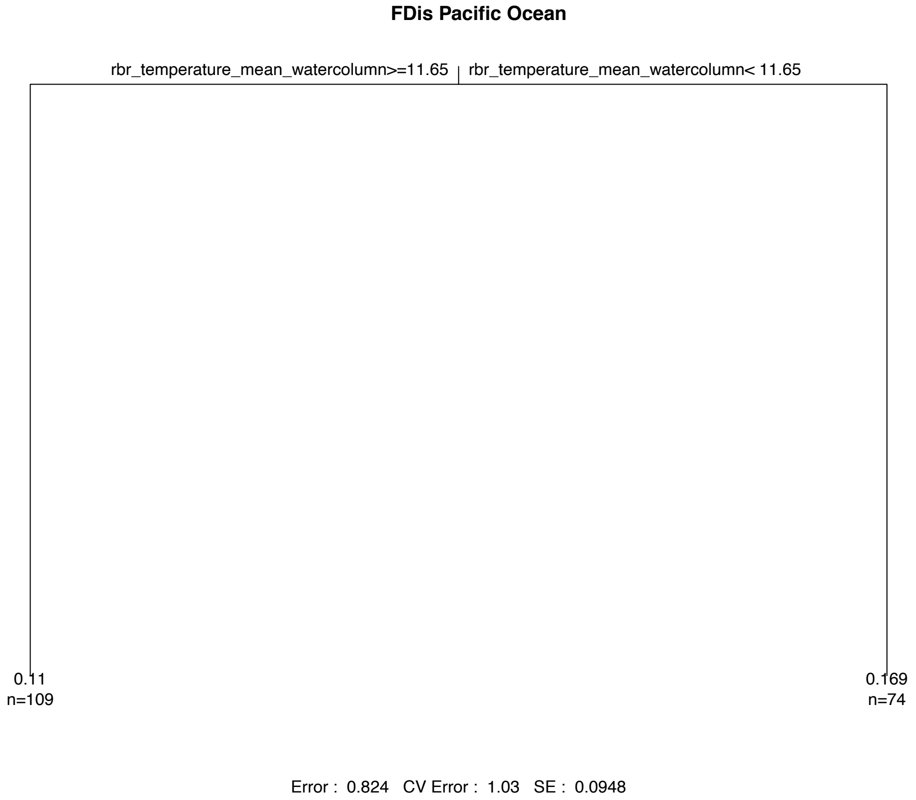
Error : 0.619 CV Error : 1.13 SE : 0.196

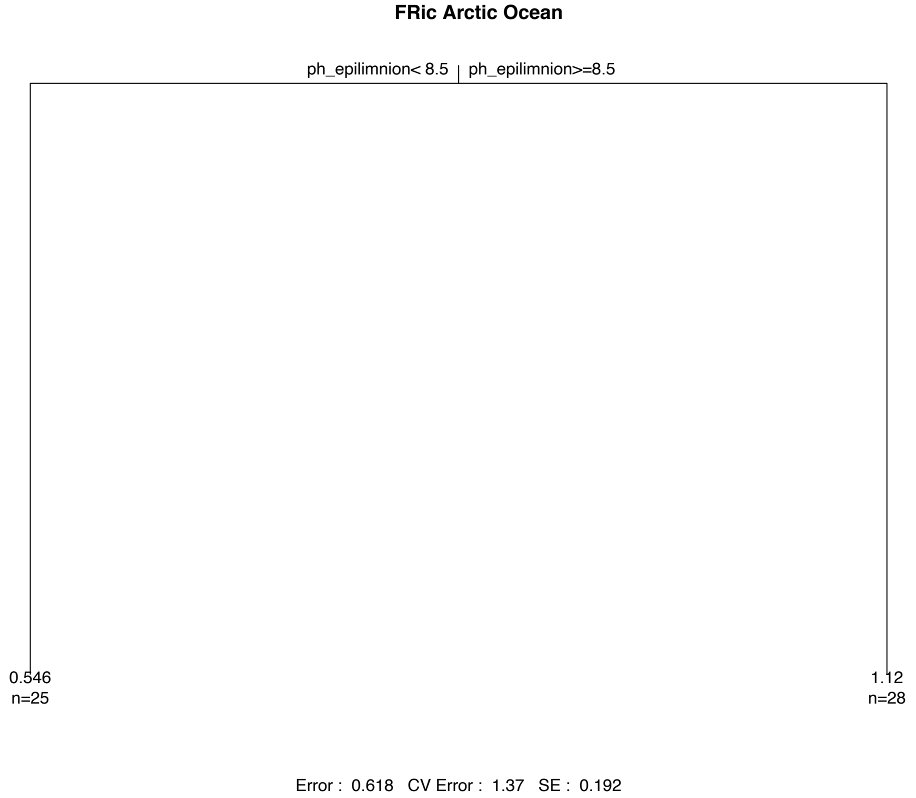
FDis Great Lakes–St. Lawrence

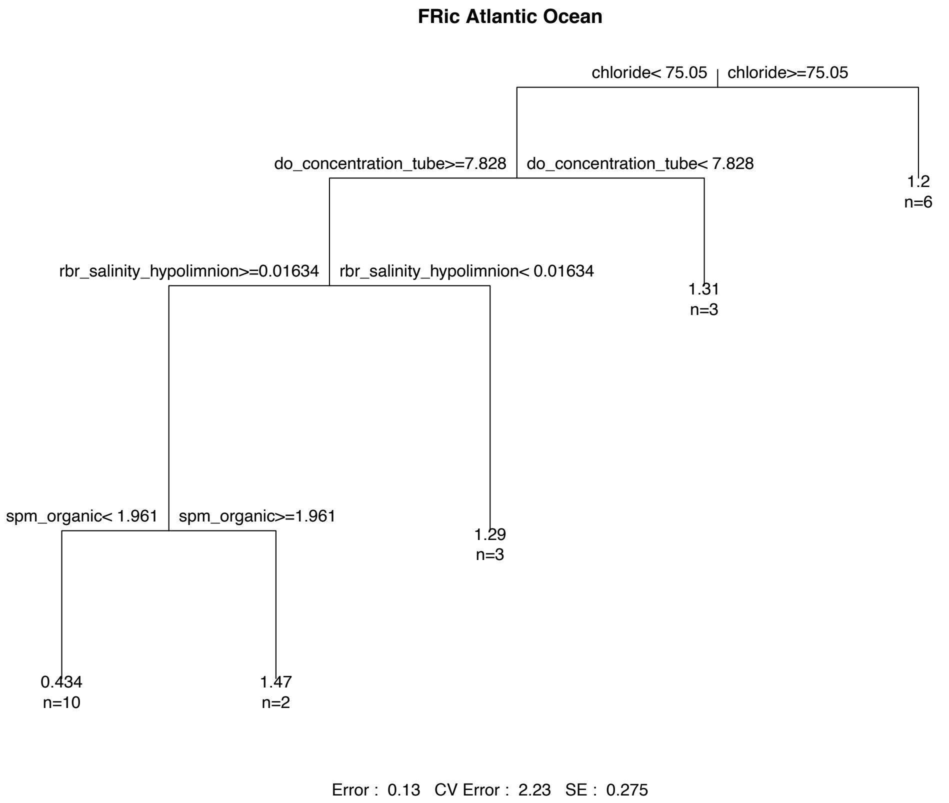


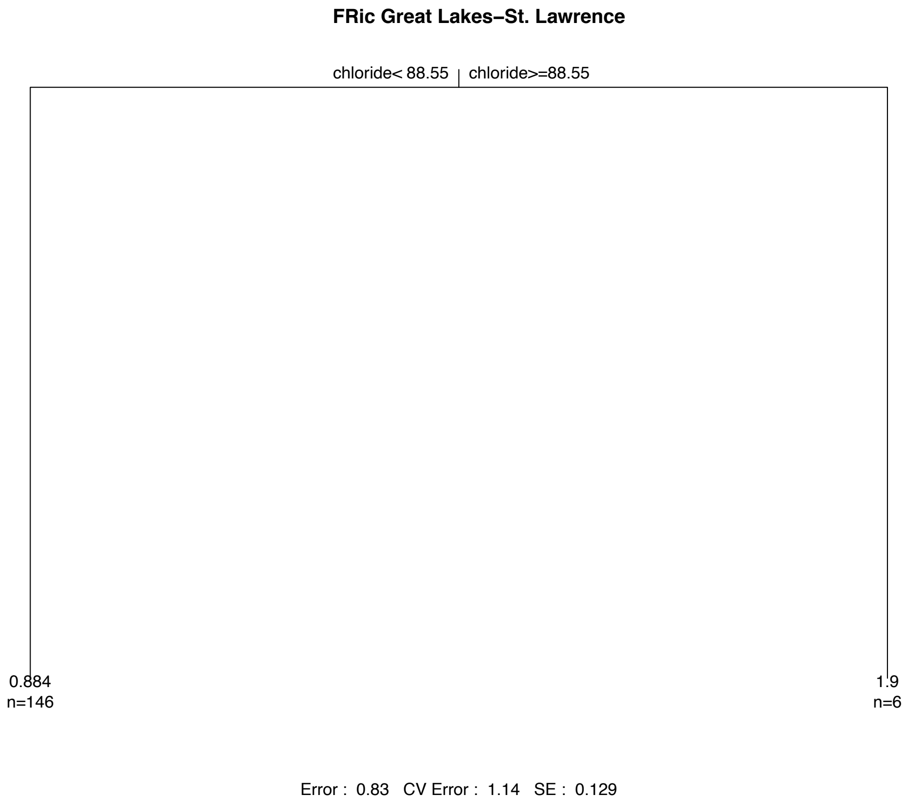
FDis Hudson Bay




FDis Pacific Ocean
rbr_temperature_mean_watercolumn>=11.65
rbr_temperature_mean_watercolumn< 11.65
0.11
n=109
0.169
n=74
Error : 0.824 CV Error : 1.03 SE : 0.0948


FRic Arctic Ocean
ph_epilimnion< 8.5
ph_epilimnion>=8.5
0.546
n=25
1.12
n=28
Error : 0.618 CV Error : 1.37 SE : 0.192


FRic Atlantic Ocean
chloride< 75.05
chloride>=75.05
do_concentration_tube>=7.828
do_concentration_tube< 7.828
1.2
n=6
rbr_salinity_hypolimnion>=0.01634
rbr_salinity_hypolimnion< 0.01634
1.31
n=3
spm_organic< 1.961
spm_organic>=1.961
1.29
n=3
0.434
n=10
1.47
n=2
Error : 0.13 CV Error : 2.23 SE : 0.275


FRic Great Lakes–St. Lawrence
chloride< 88.55
chloride>=88.55
0.884
n=146
1.9
n=6
Error : 0.83 CV Error : 1.14 SE : 0.129

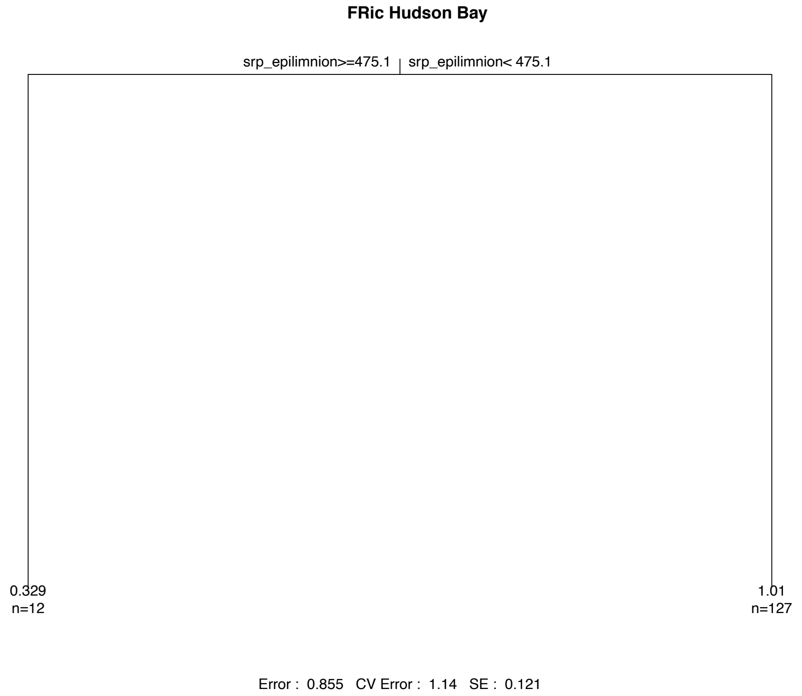


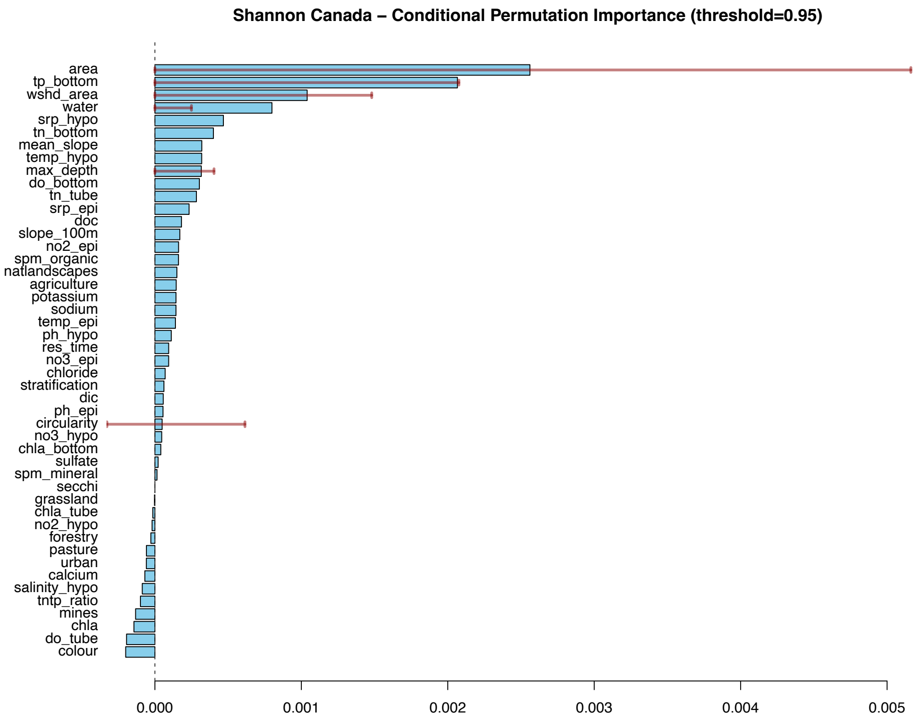
Figure H.1 URT plots of taxonomic and functional diversity indices across Canada and by continental basin. Below each plot, the error, cross-validated error (CV error) and standard error (SE) are provided. Diversity indices abbreviations are as follow: Shannon diversity (H) Simpson diversity (Sim) Evenness (J) Total richness (Svegan) Rarefied richness (Rarefied1) Functional evenness (FEve) Functional dispersion (FDis) Functional richness (FRic).

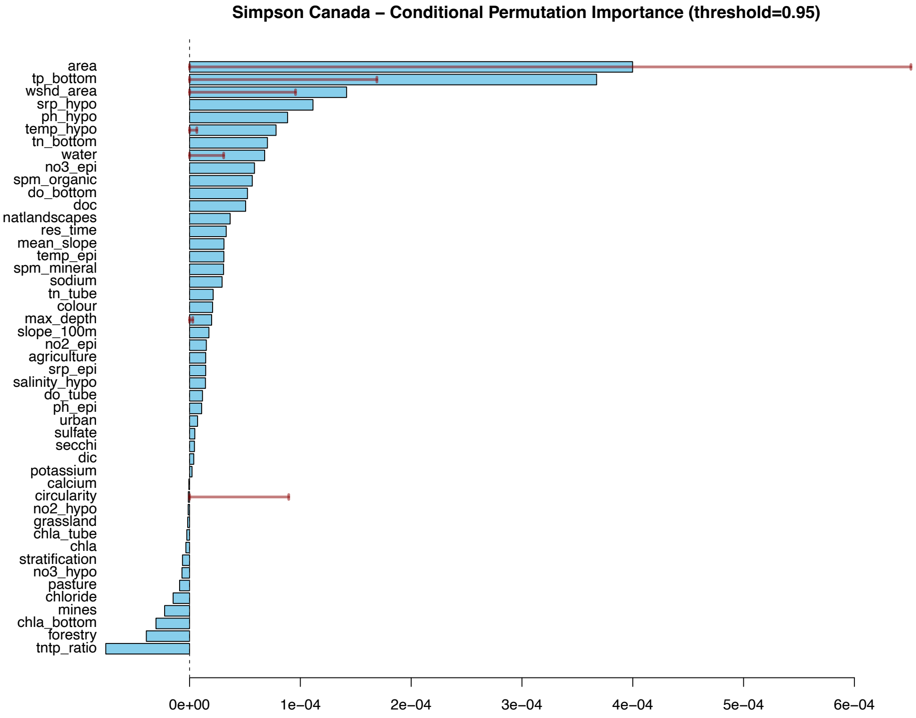
ANNEXE I

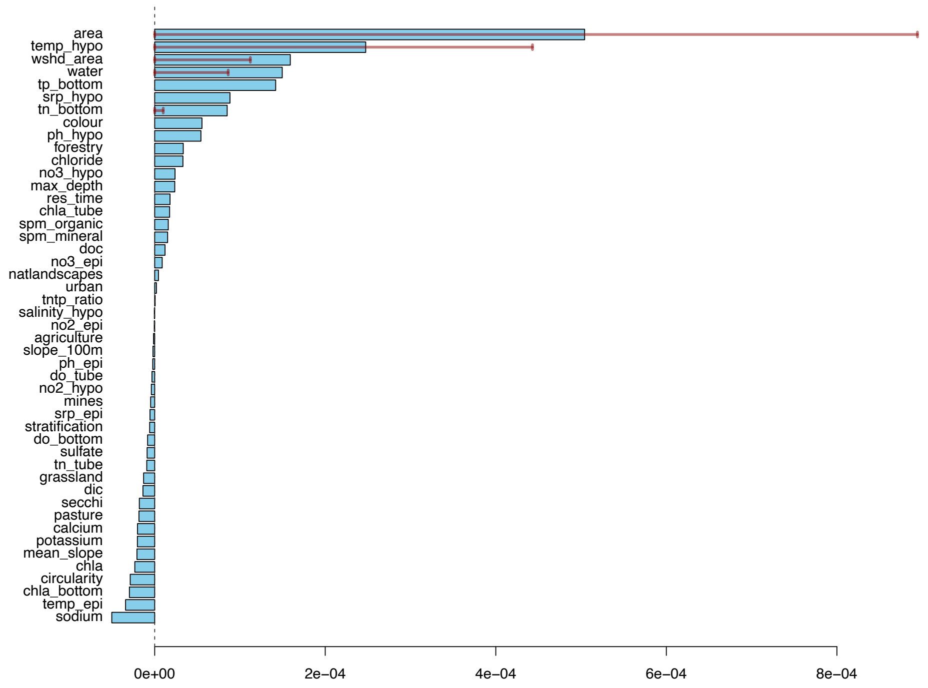
RANDOM FOREST CONDITIONAL PERMUTATION IMPORTANCE ACROSS CANADA BY DIVERSITY INDICES

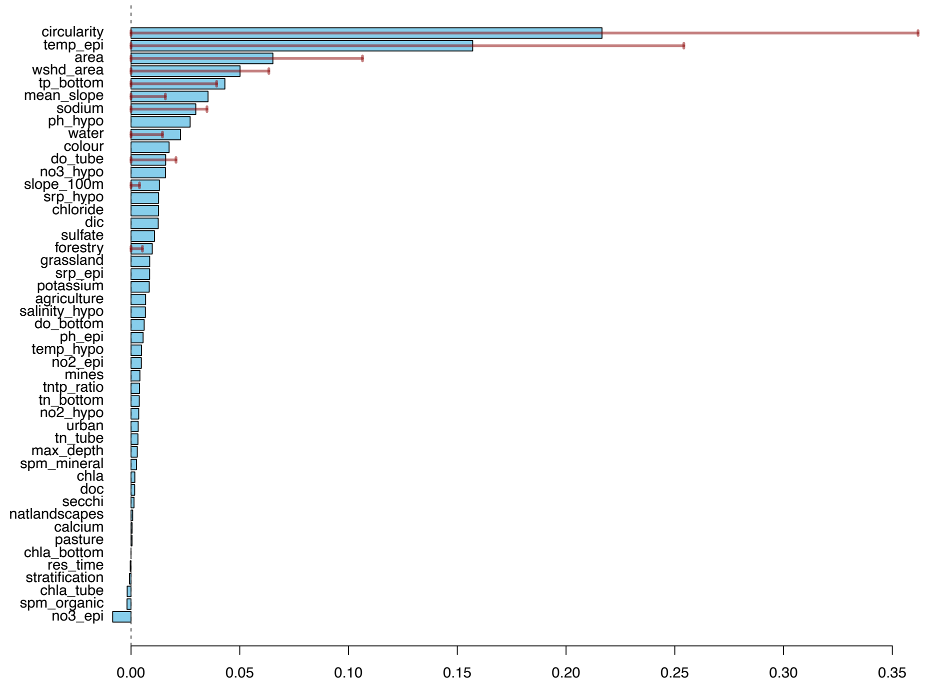
Table I2: Taxonomic and functional diversity indices along with the R^2 and p and first variable selected from the Random Forest models. The largest value is highlighted in bold.

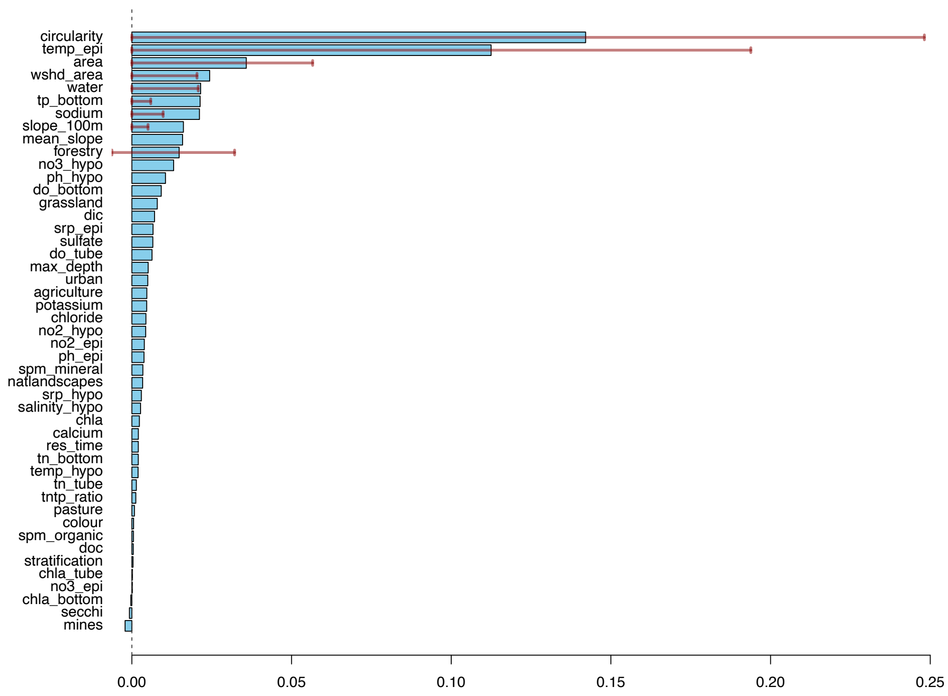
Diversity index	R^2	First variable
Shannon	0.15	area
Simpson	0.08	area
Evenness	0.04	area
Richness	0.24	circularity
Rarefied Richness	**0.27**	circularity
Functional richness	0.16	area
Functional Evenness	0.01	fraction water
Functional dispersion	0.13	TP_bottom

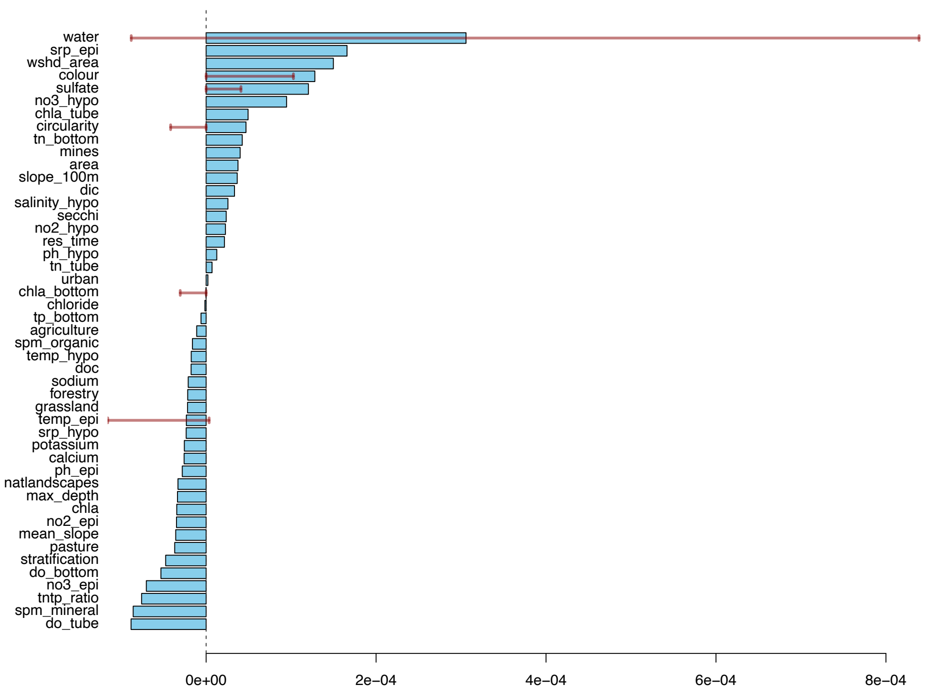

Shannon Canada – Conditional Permutation Importance (threshold=0.95)


Simpson Canada – Conditional Permutation Importance (threshold=0.95)


Evenness Canada – Conditional Permutation Importance (threshold=0.95)


Richness Canada – Conditional Permutation Importance (threshold=0.95)


Rarefied richness Canada – Conditional Permutation Importance (threshold=0.95)


FEve Canada – Conditional Permutation Importance (threshold=0.95)

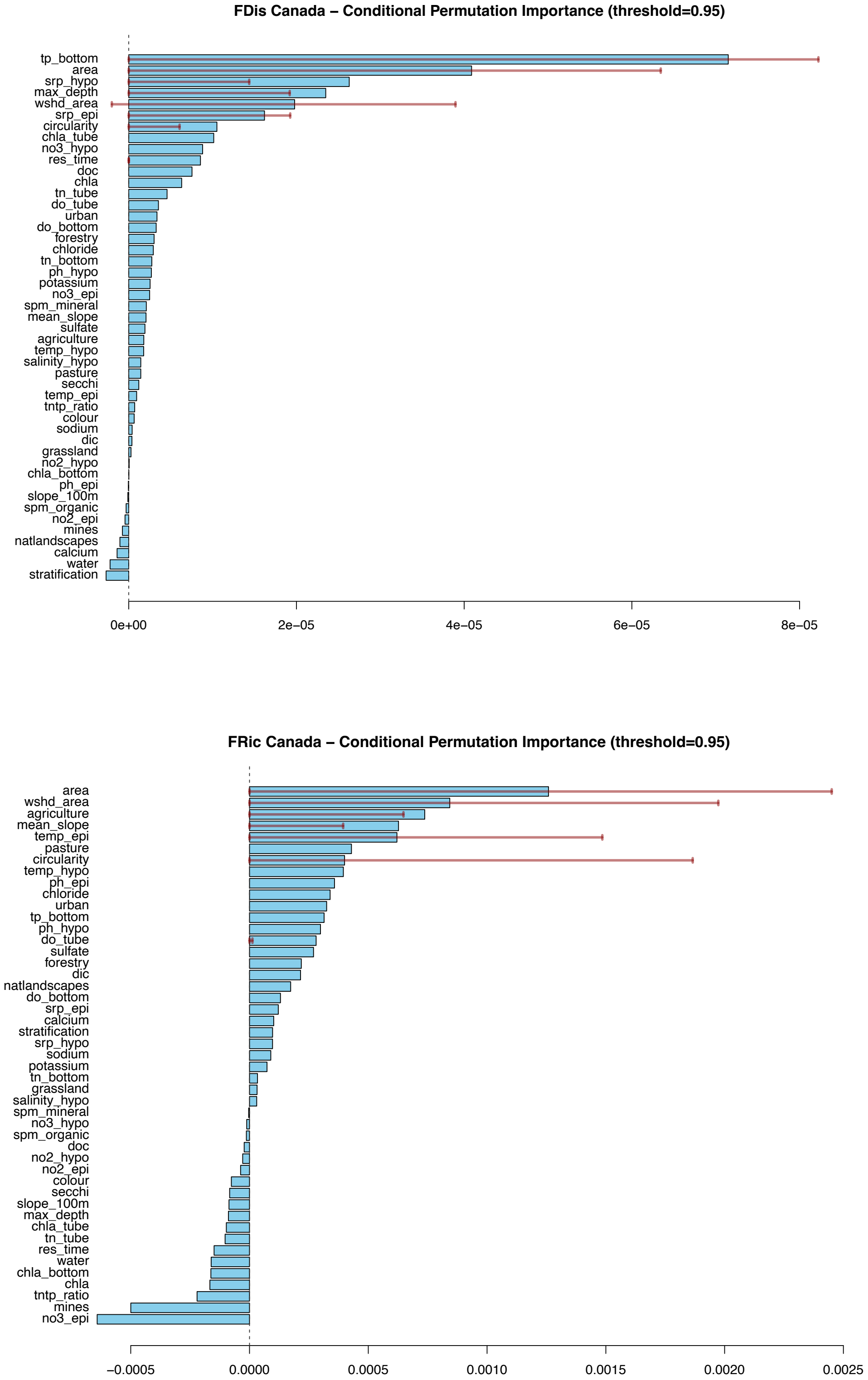
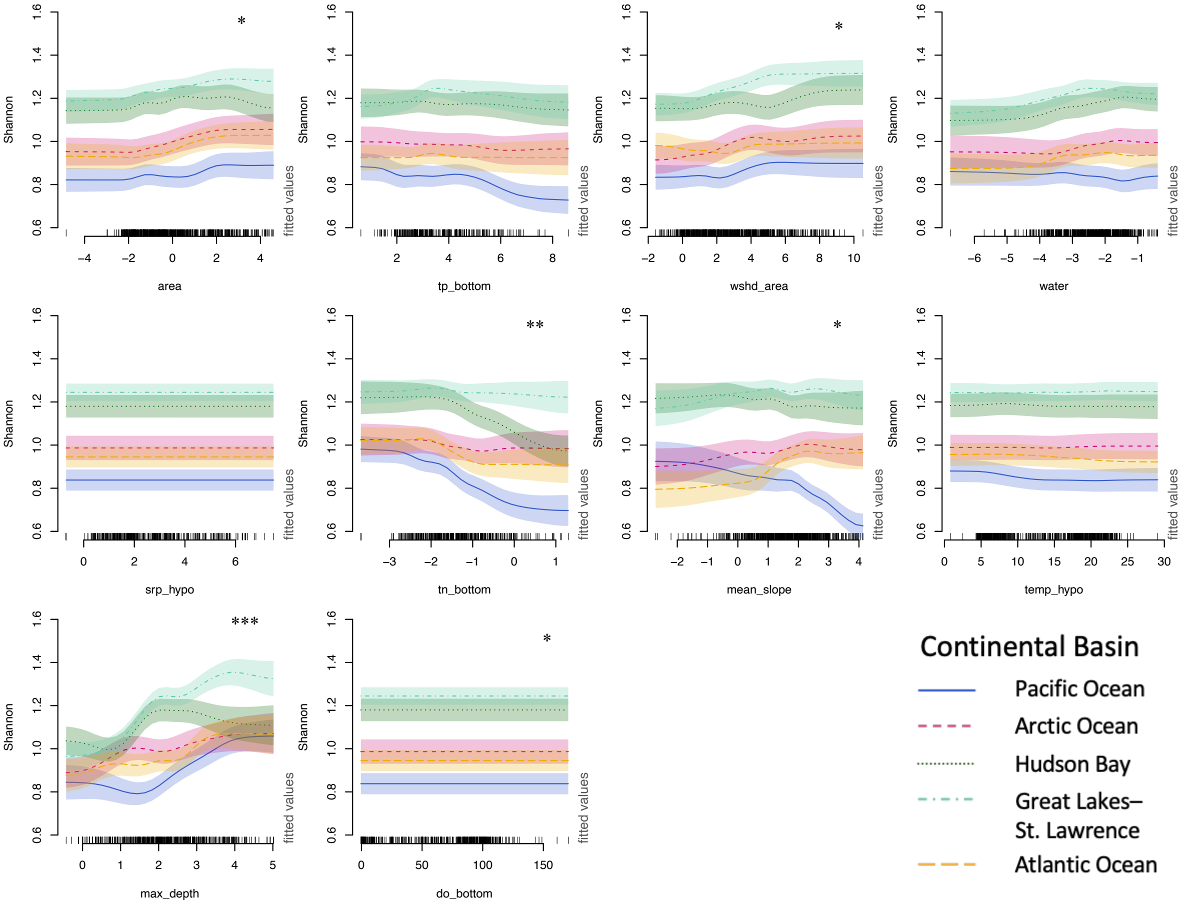


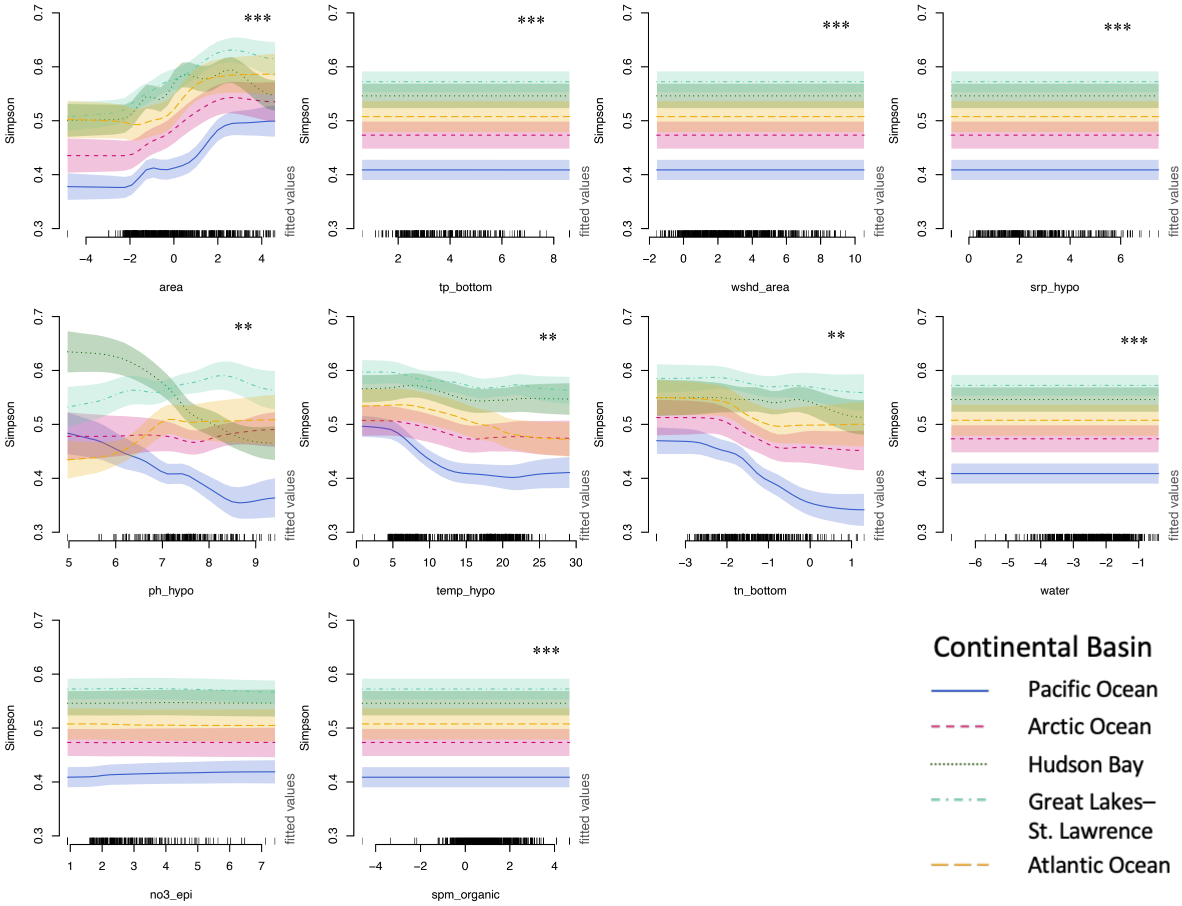
Figure I.1 Conditional permutation importance barplots by diversity indices across Canada. Red error bars represent the .25 and .75 quantiles of the perTree values.

ANNEXE J
GENERAL ADDITIVE MIXED MODEL (GAMM)

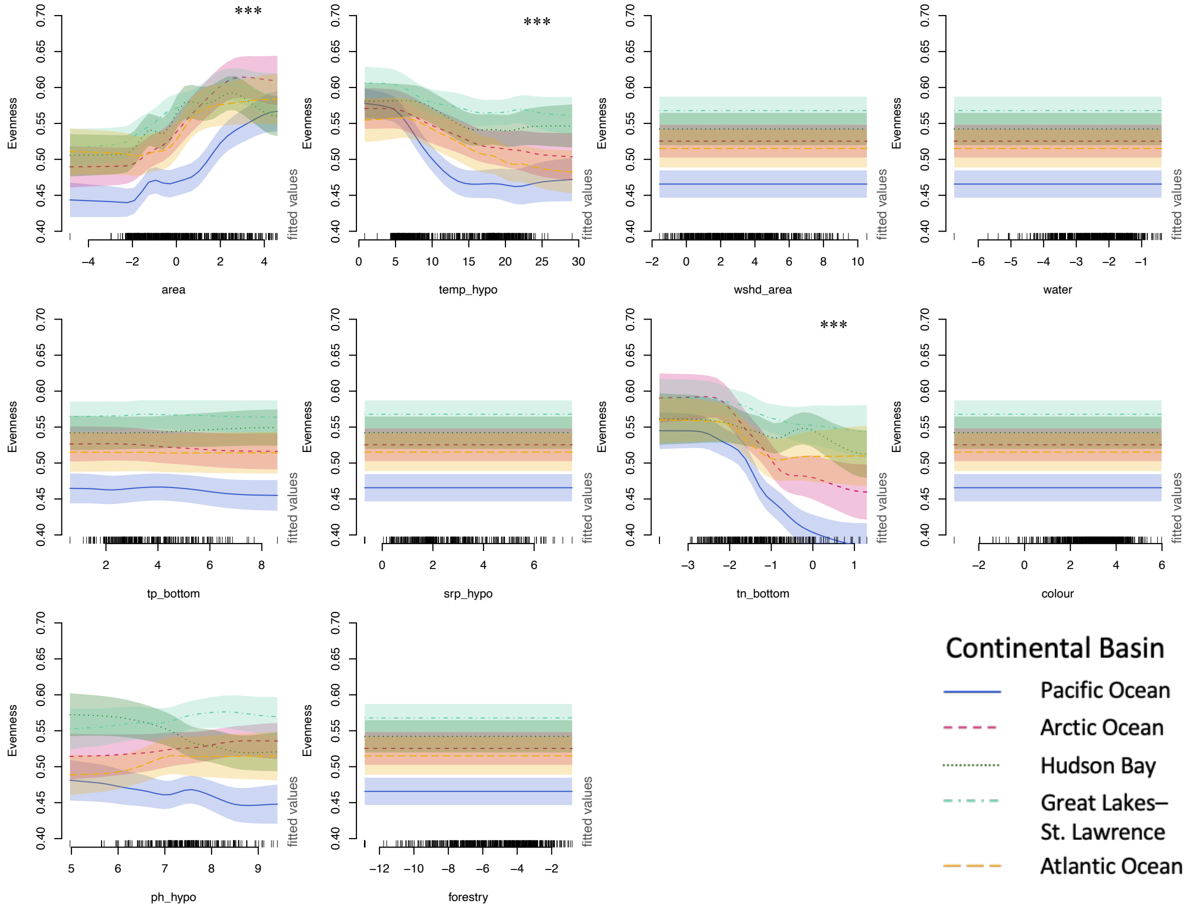
a) Shannon diversity



b) Simpson diversity

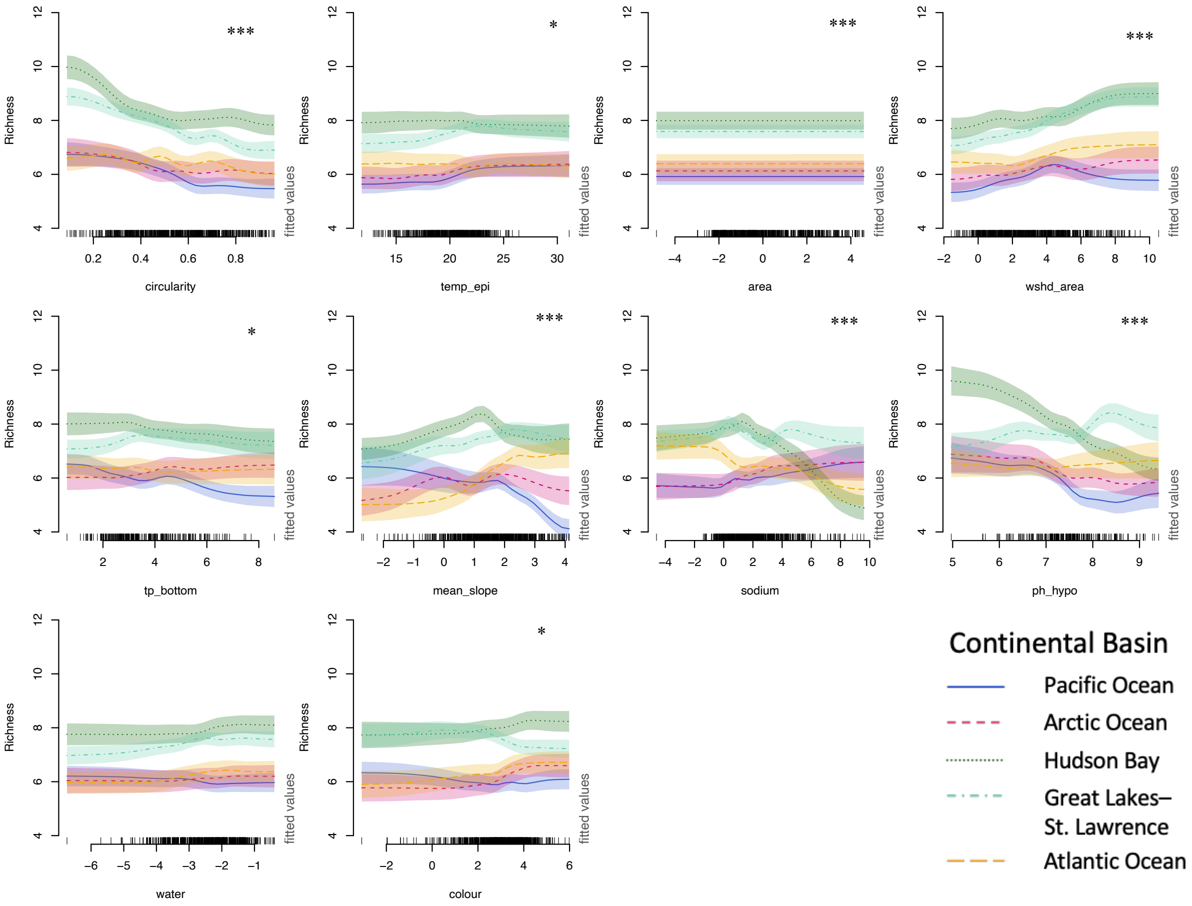


c) Evenness



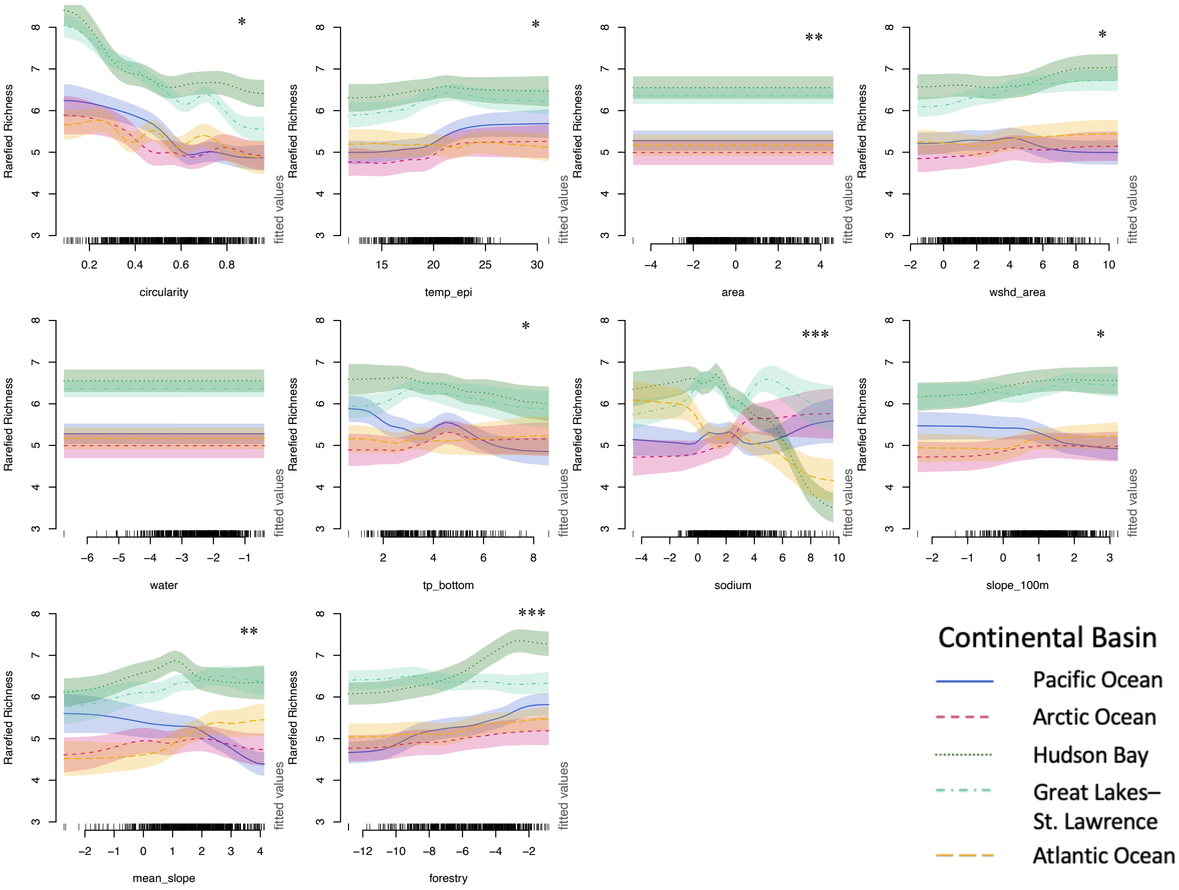
Evenness
fitted values
0.40
0.45
0.50
0.55
0.60
0.65
0.70
***
area
temp_hypo
wshd_area
water
tp_bottom
srp_hypo
tn_bottom
colour
ph_hypo
forestry
Continental Basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–
St. Lawrence
Atlantic Ocean

d) Richness

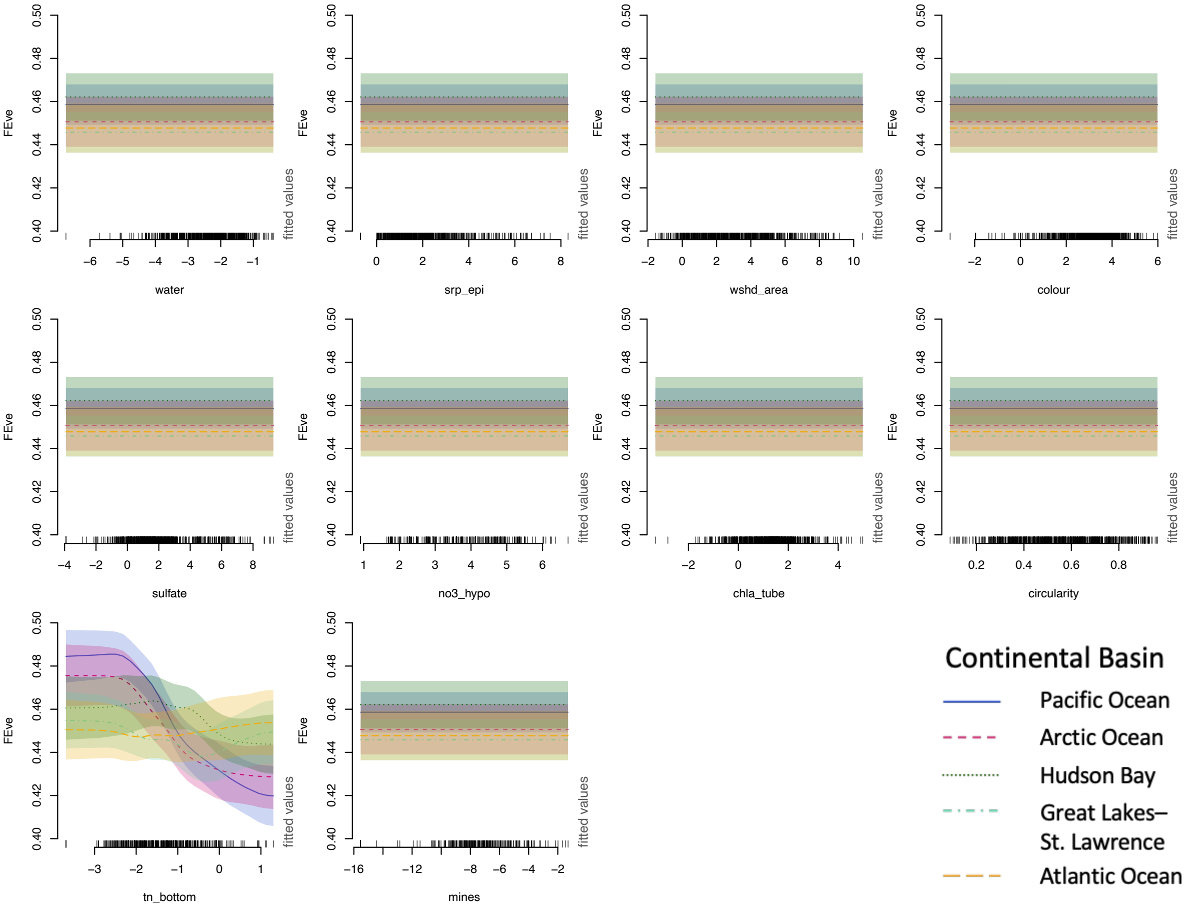


Richness
12
10
8
6
4
fitted values
***
0.2
0.4
0.6
0.8
circularity
*
15
20
25
30
temp_epi
***
−4
−2
0
2
4
area
***
−2
0
2
4
6
8
10
wshd_area
*
2
4
6
8
tp_bottom
***
−2
−1
0
1
2
3
4
mean_slope
***
−4
−2
0
2
4
6
8
10
sodium
***
5
6
7
8
9
ph_hypo
−6
−5
−4
−3
−2
−1
water
*
−2
0
2
4
6
colour
Continental Basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean

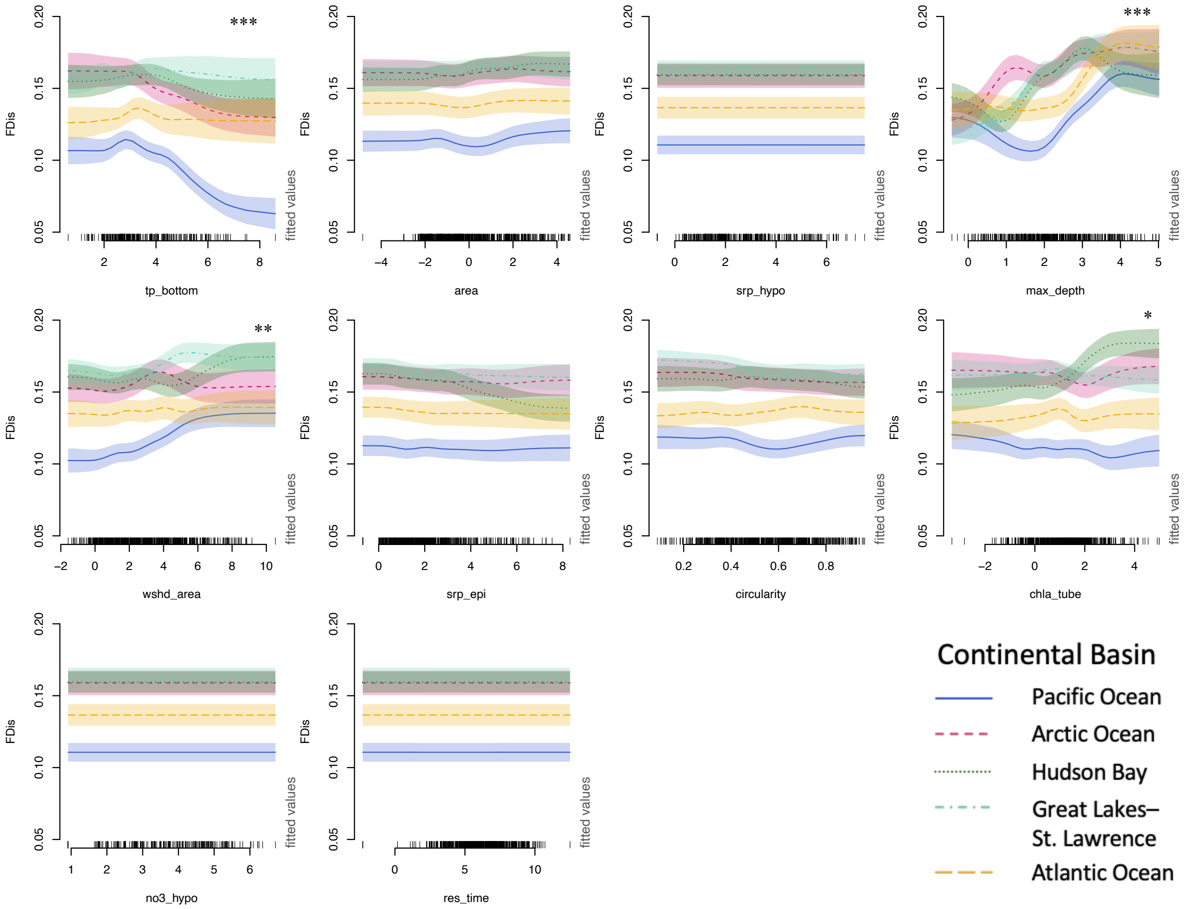
e) Rarefied richness



f) Functional evenness



g) Functional dispersion



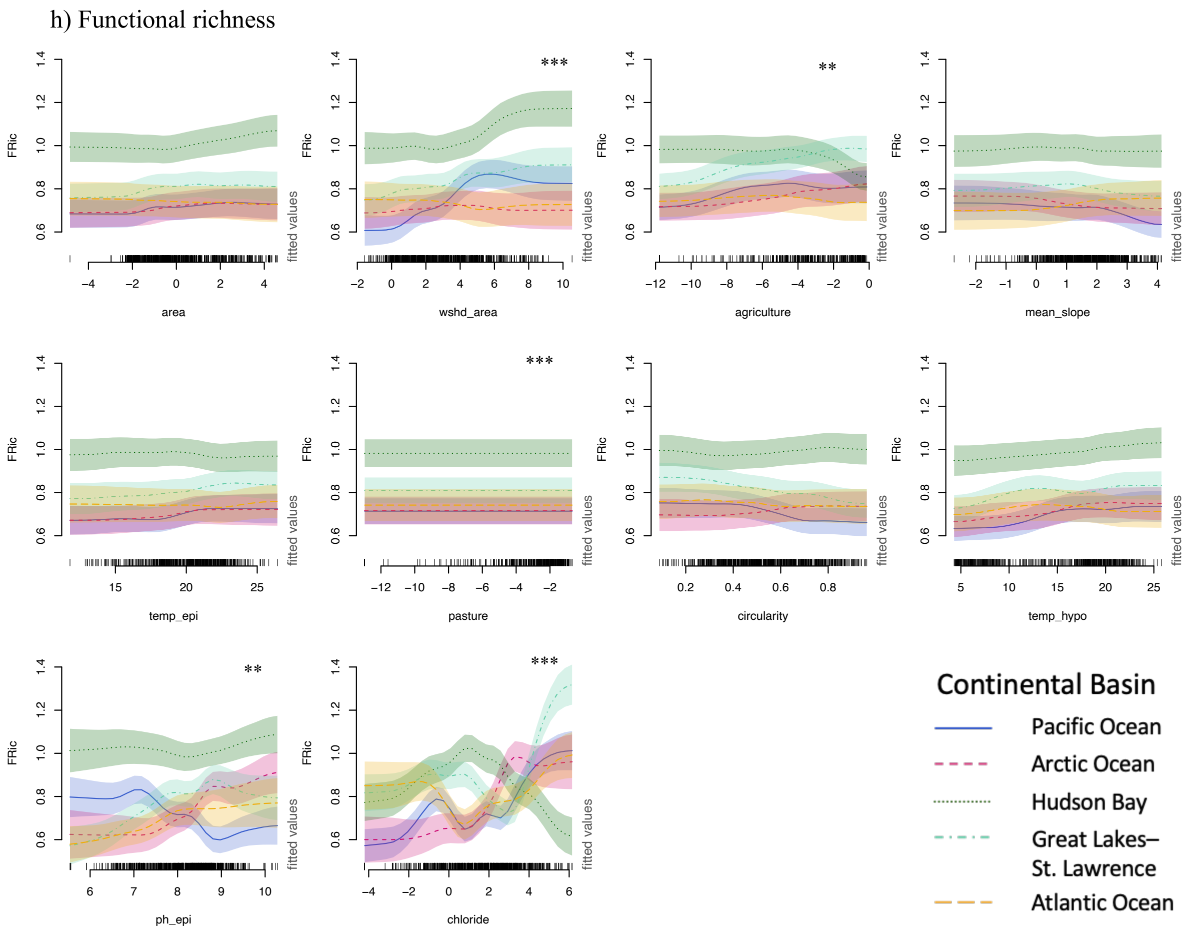

h) Functional richness

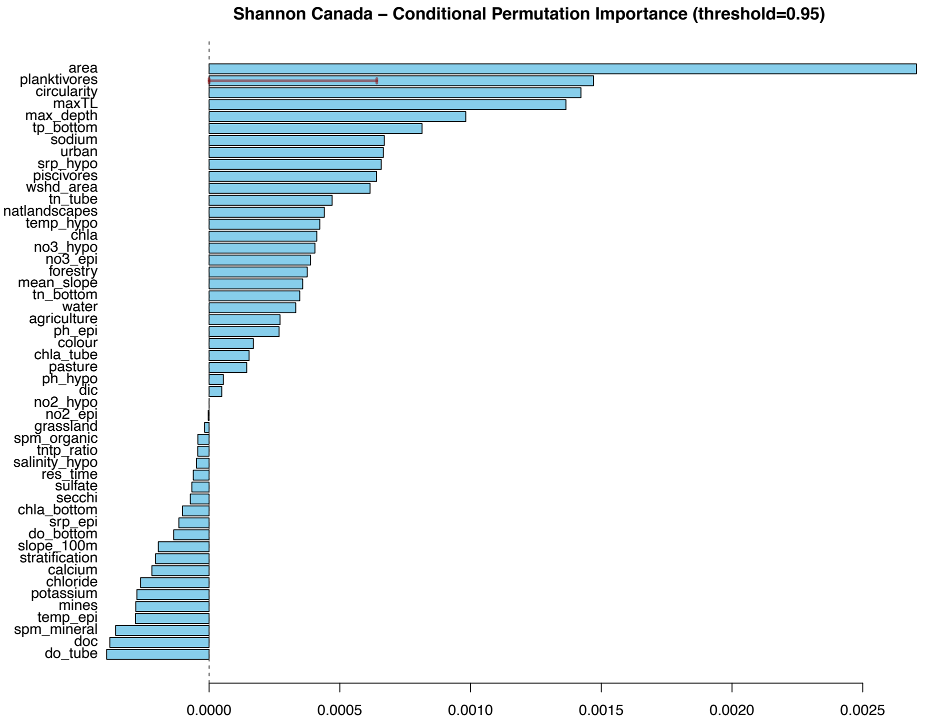
Figure J.1 General additive mixed model (GAMM) plots of fitted (a) Shannon diversity, (b) Simpson diversity, (c) Evenness, (d) richness, (e) rarefied richness, (f) functional evenness, (g) functional dispersion and (h) functional richness values against the ten most important predictors as sorted by Random Forest (RF) model, with continental basins as random smooth factor. Shaded area represents the confidence interval, reduced at se=0.5 to aid visualisation. *p-value<0.05; **p-value<0.01; ***p-value<0.001.

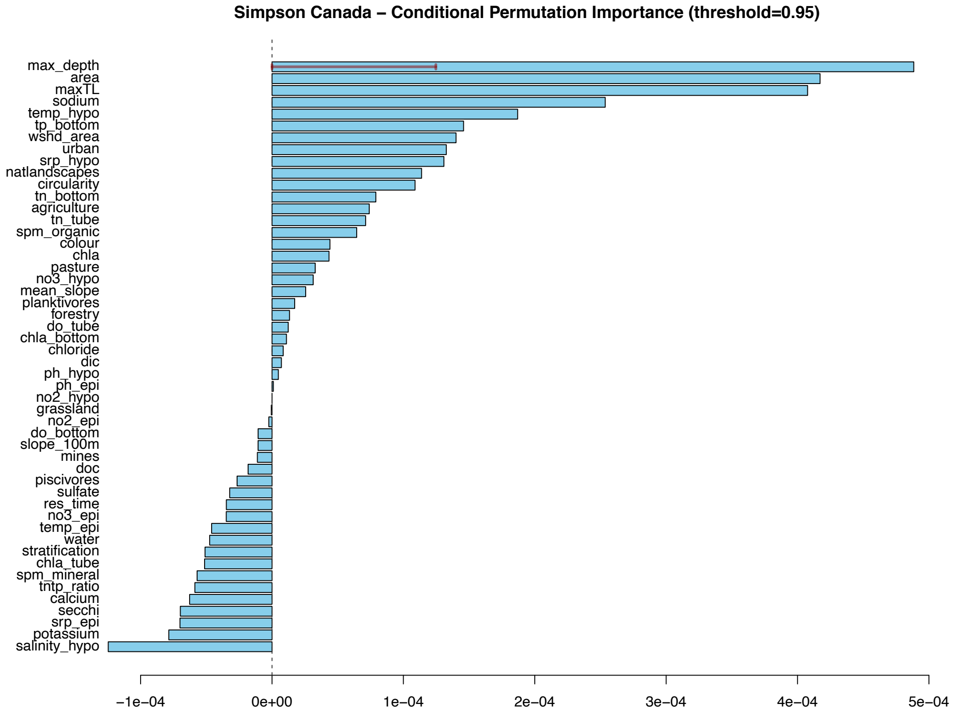
ANNEXE K

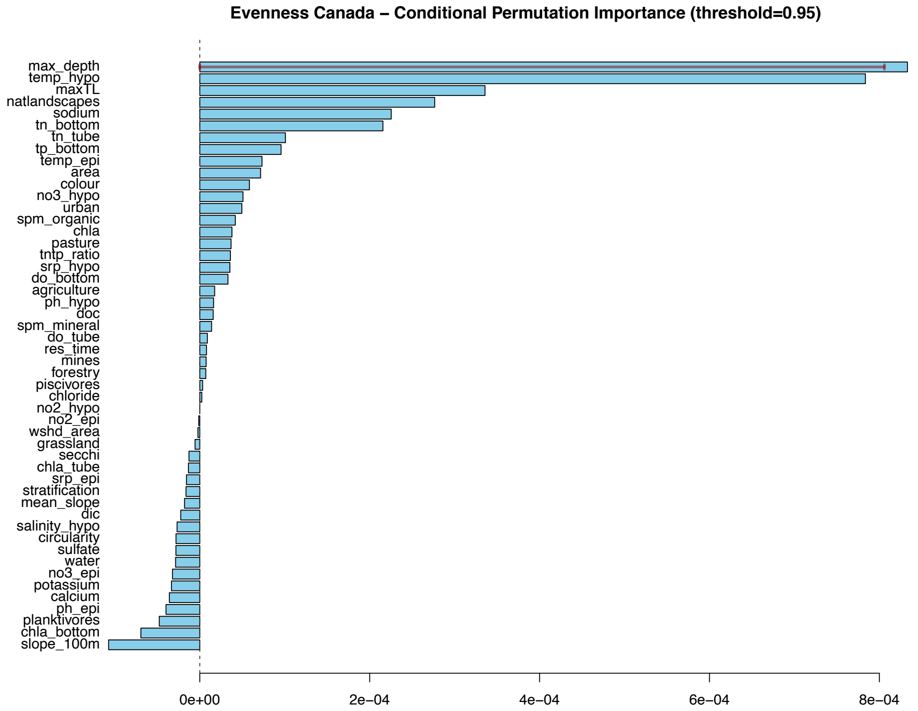
RANDOM FOREST CONDITIONAL PERMUTATION IMPORTANCE ACROSS CANADA BY DIVERSITY INDICES FROM THE REDUCED 314 LAKE DATASET WITH FISH VARIABLES

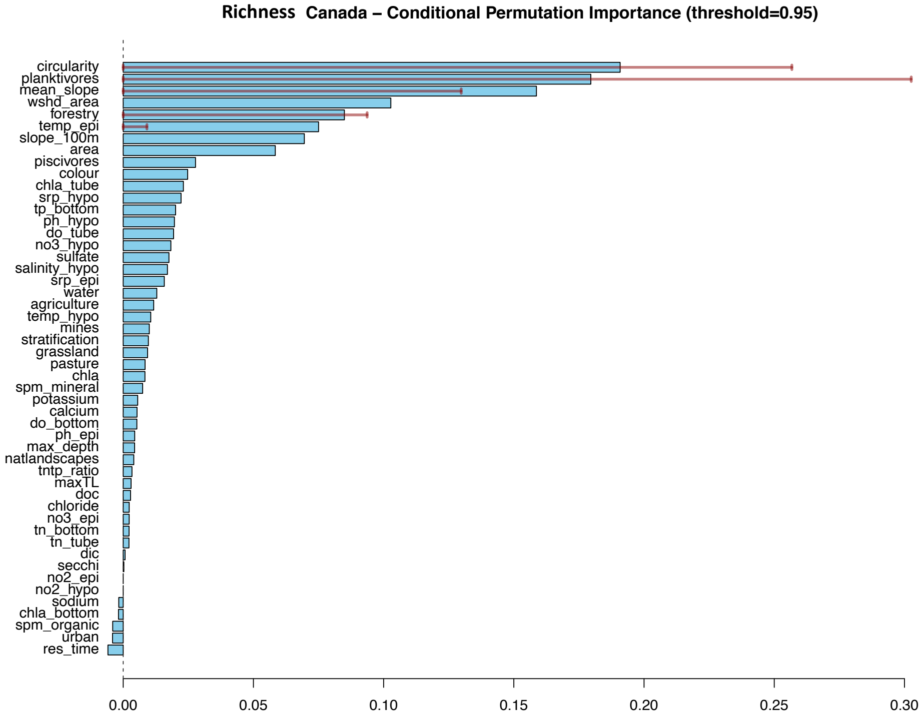
Table K.1 Taxonomic and functional diversity indices along with the R^2 and p and first variable selected from the Random Forest models from the reduced 314 lake dataset. The largest value is highlighted in bold.

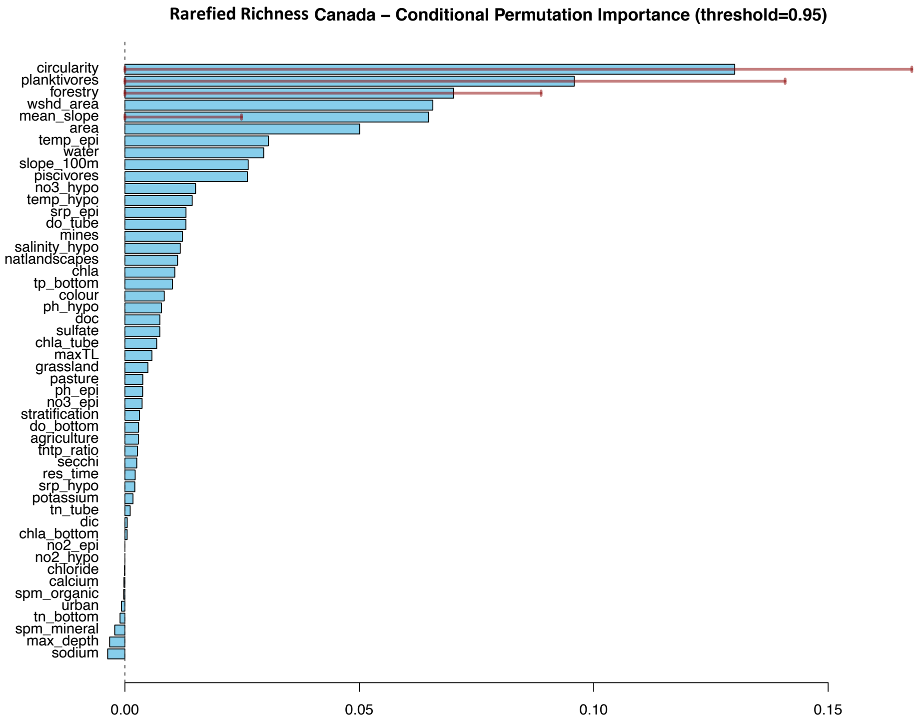
Diversity index	R^2	First variable
Shannon	0.02	Area
Simpson	0.002	Depth
Evenness	0.005	Depth
Richness	0.12	Circularity
Rarefied Richness	0.07	Circularity
Functional richness	0.08	Planktivore richness
Functional Evenness	0.01	Pasture
Functional dispersion	**0.16**	Depth

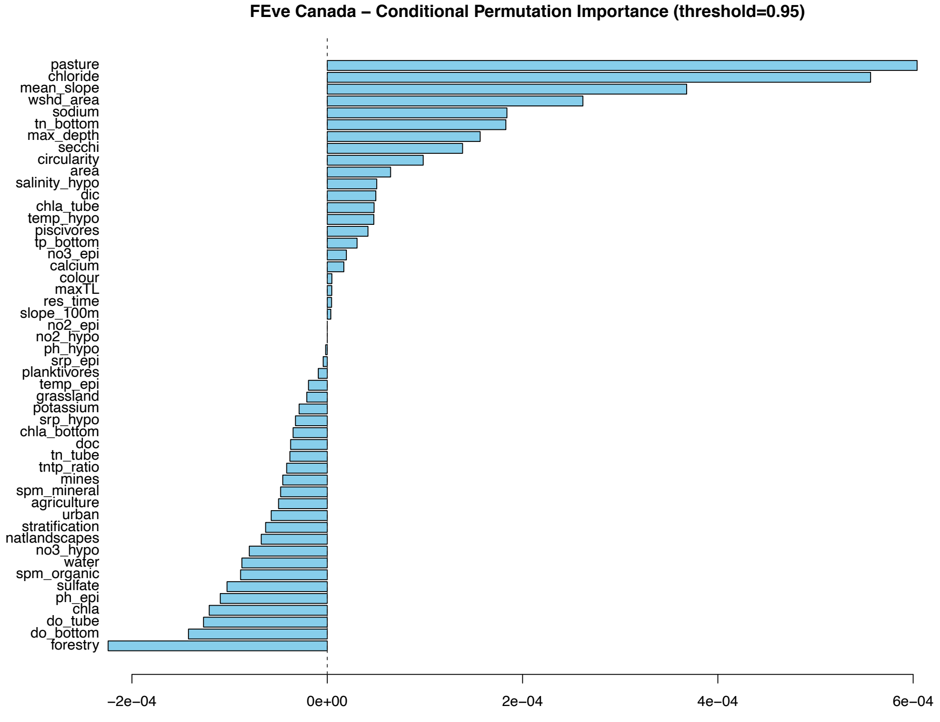

Shannon Canada – Conditional Permutation Importance (threshold=0.95)
area
planktivores
circularity
maxTL
max_depth
tp_bottom
sodium
urban
srp_hypo
piscivores
wshd_area
tn_tube
natlandscapes
temp_hypo
chla
no3_hypo
no3_epi
forestry
mean_slope
tn_bottom
water
agriculture
ph_epi
colour
chla_tube
pasture
ph_hypo
dic
no2_hypo
no2_epi
grassland
spm_organic
tntp_ratio
salinity_hypo
res_time
sulfate
secchi
chla_bottom
srp_epi
do_bottom
slope_100m
stratification
calcium
chloride
potassium
mines
temp_epi
spm_mineral
doc
do_tube
0.0000
0.0005
0.0010
0.0015
0.0020
0.0025


Simpson Canada – Conditional Permutation Importance (threshold=0.95)
max_depth
area
maxTL
sodium
temp_hypo
tp_bottom
wshd_area
urban
srp_hypo
natlandscapes
circularity
tn_bottom
agriculture
tn_tube
spm_organic
colour
chla
pasture
no3_hypo
mean_slope
planktivores
forestry
do_tube
chla_bottom
chloride
dic
ph_hypo
ph_epi
no2_hypo
grassland
no2_epi
do_bottom
slope_100m
mines
doc
piscivores
sulfate
res_time
no3_epi
temp_epi
water
stratification
chla_tube
spm_mineral
tntp_ratio
calcium
secchi
srp_epi
potassium
salinity_hypo
−1e−04
0e+00
1e−04
2e−04
3e−04
4e−04
5e−04


Evenness Canada – Conditional Permutation Importance (threshold=0.95)


Richness Canada – Conditional Permutation Importance (threshold=0.95)


Rarefied Richness Canada – Conditional Permutation Importance (threshold=0.95)


FEve Canada – Conditional Permutation Importance (threshold=0.95)

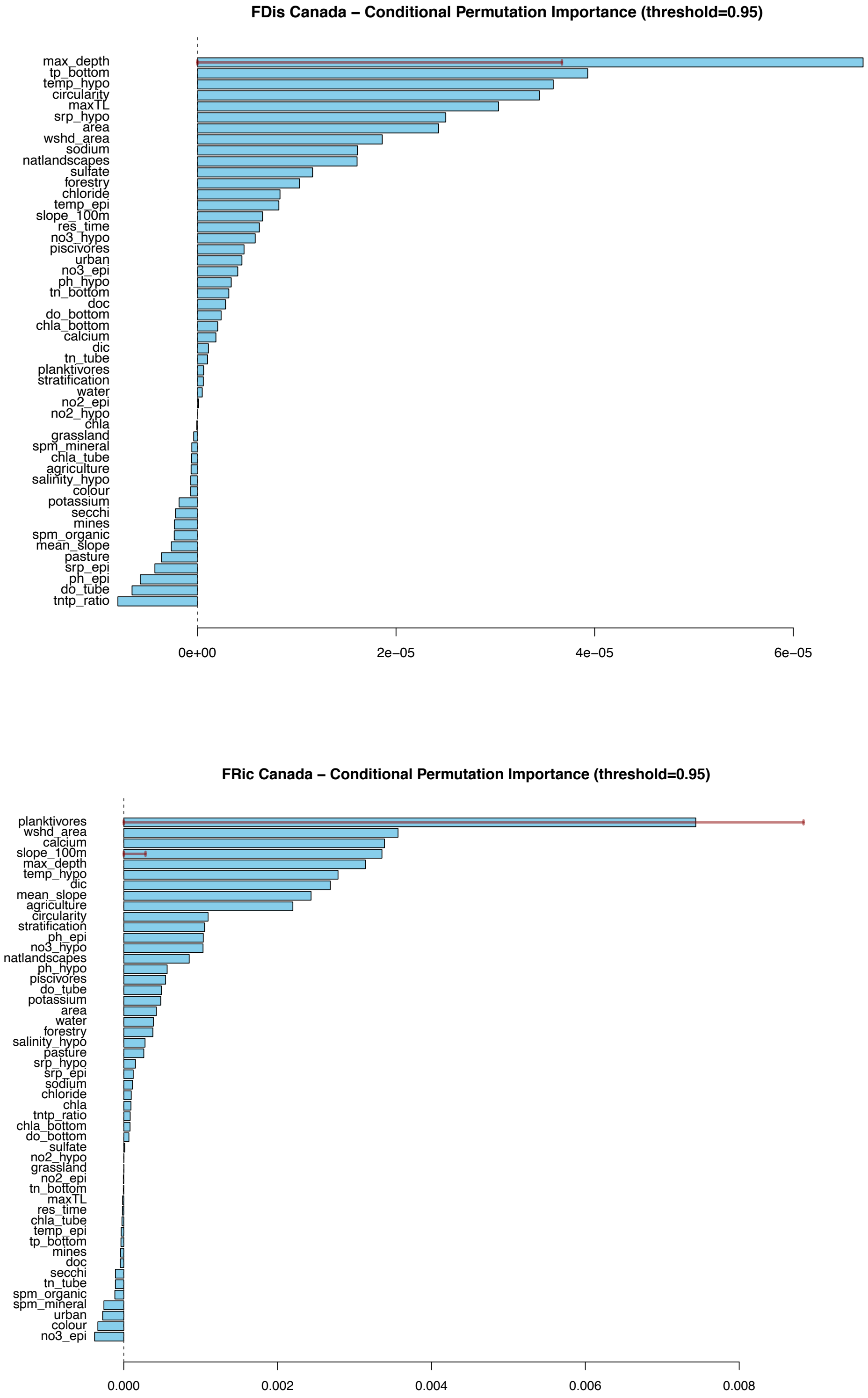


Figure K.1 Conditional permutation importance barplots by diversity indices across Canada from the reduced 314 lakes dataset. Red error bars represent the .25 and .75 quantiles of the perTree values.

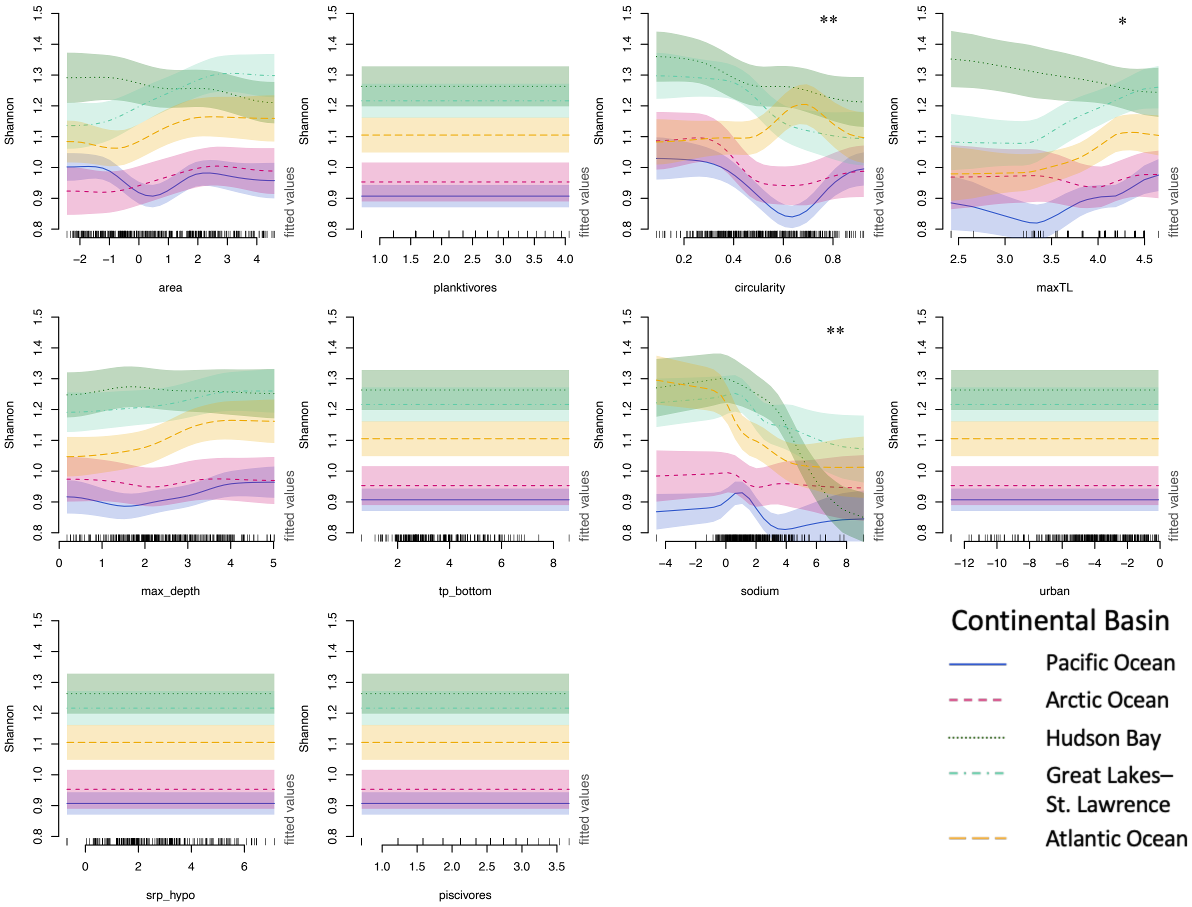
ANNEXE L

GENERAL ADDITIVE MIXED MODEL (GAMM) PLOTS INDICES FROM THE REDUCED 314 LAKE DATASET

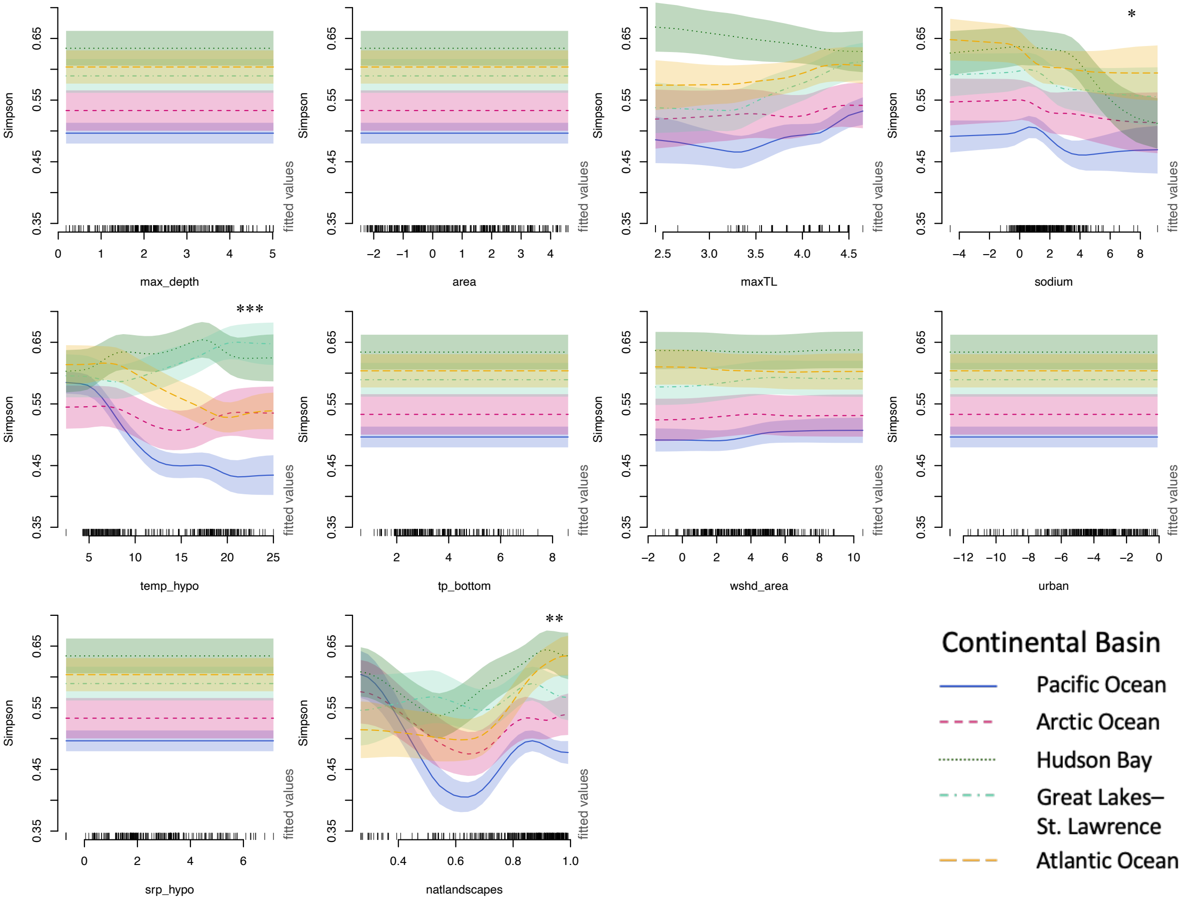
Table L.1 Taxonomic and functional diversity indices along with the R^2 and percentage of deviance explained (separated by -) and variable of greatest importance with respective *p-values* in parentheses from the General additive mixed models (GAMMs) of the reduced 314 lakes dataset with fish variables. The ten most important variables selected by random forest (RF) were used for each diversity index GAMM, and continental basin was used as a random smooth factor. The greatest value across all diversity indices is highlighted in bold.

Diversity index	**R^2 - % deviance explained**	**Variable of greatest importance (*p*-value)**
Shannon	0.18 – 24.2%	Sodium (0.003)
Simpson	0.18 – 24.5%	Temp_hypo (0.0001)
Evenness	0.16 – 21.8%	Temp_hypo (7.07e-05)
Richness	**0.39 - 46.3%**	Mean_slope (6.68e-06)
Rarefied richness	0.32 – 39.7%	Mean_slope (5.22e-06)
Functional Evenness	0.02 – 2.78%	Pasture (0.04)
Functional dispersion	0.28 – 36.0%	Temp_hypo (8.35e-06)
Functional richness	0.29 – 36.3%	Planktivore richness (0.001)

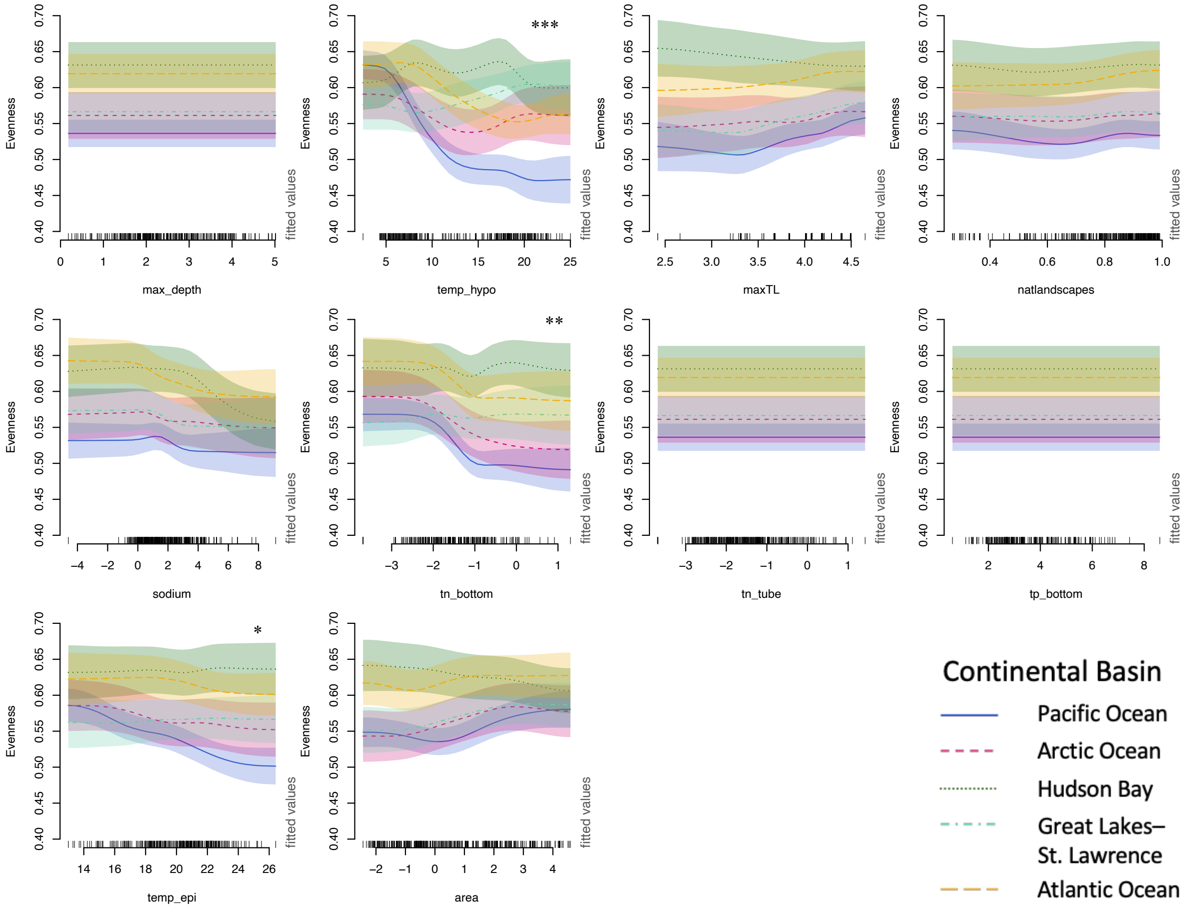
a) Shannon diversity



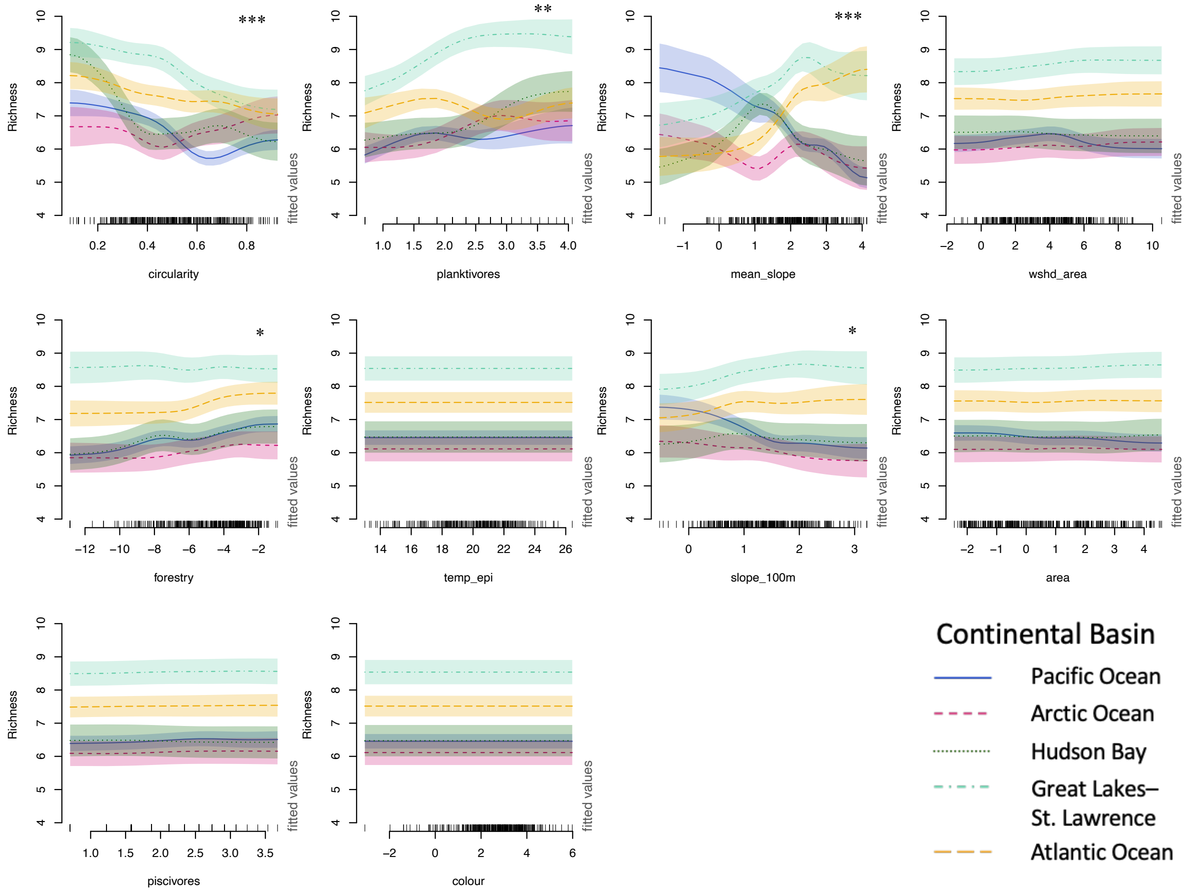
b) Simpson diversity



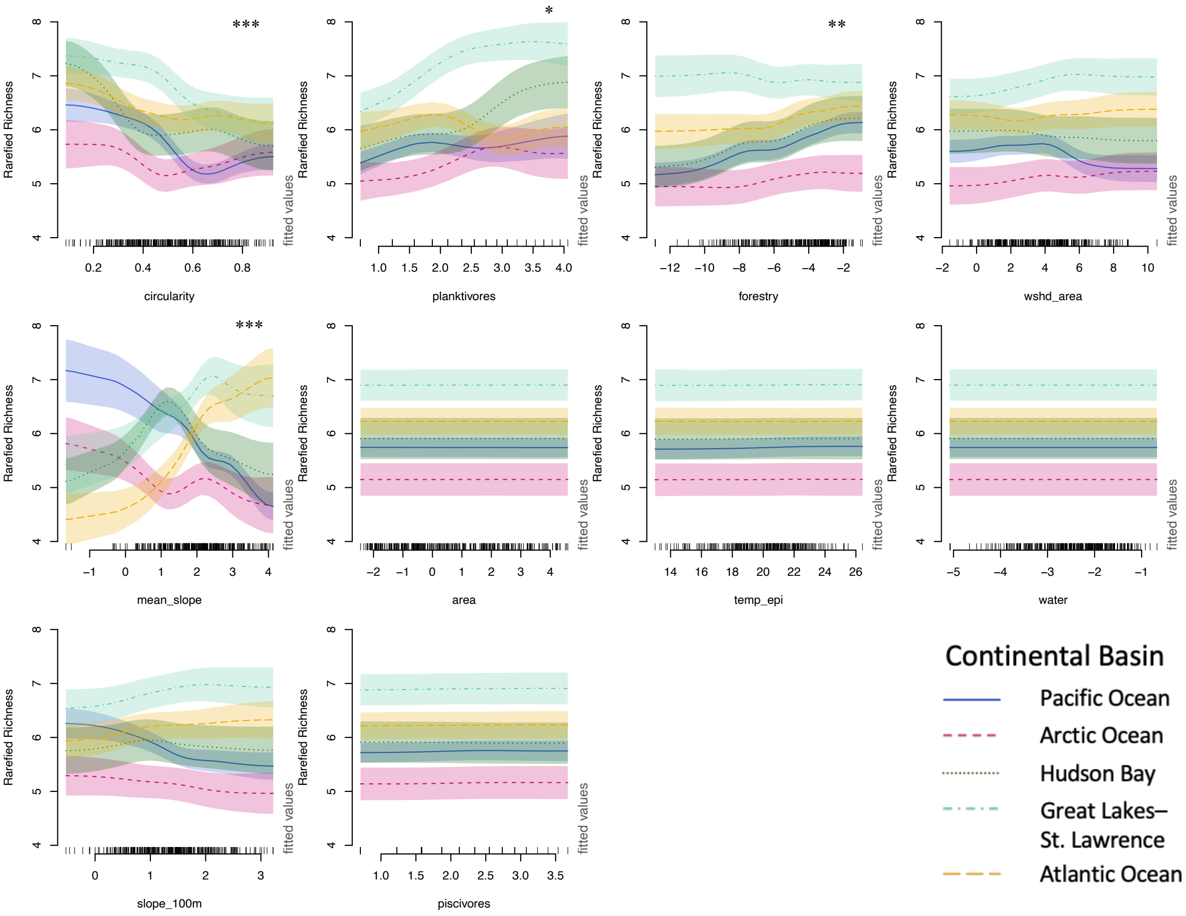
c) Evenness


Evenness
fitted values
0.40
0.45
0.50
0.55
0.60
0.65
0.70
max_depth
0 1 2 3 4 5
temp_hypo
5 10 15 20 25
***
maxTL
2.5 3.0 3.5 4.0 4.5
natlandscapes
0.4 0.6 0.8 1.0
sodium
−4 −2 0 2 4 6 8
tn_bottom
−3 −2 −1 0 1
**
tn_tube
−3 −2 −1 0 1
tp_bottom
2 4 6 8
temp_epi
14 16 18 20 22 24 26
*
area
−2 −1 0 1 2 3 4
Continental Basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–St. Lawrence
Atlantic Ocean

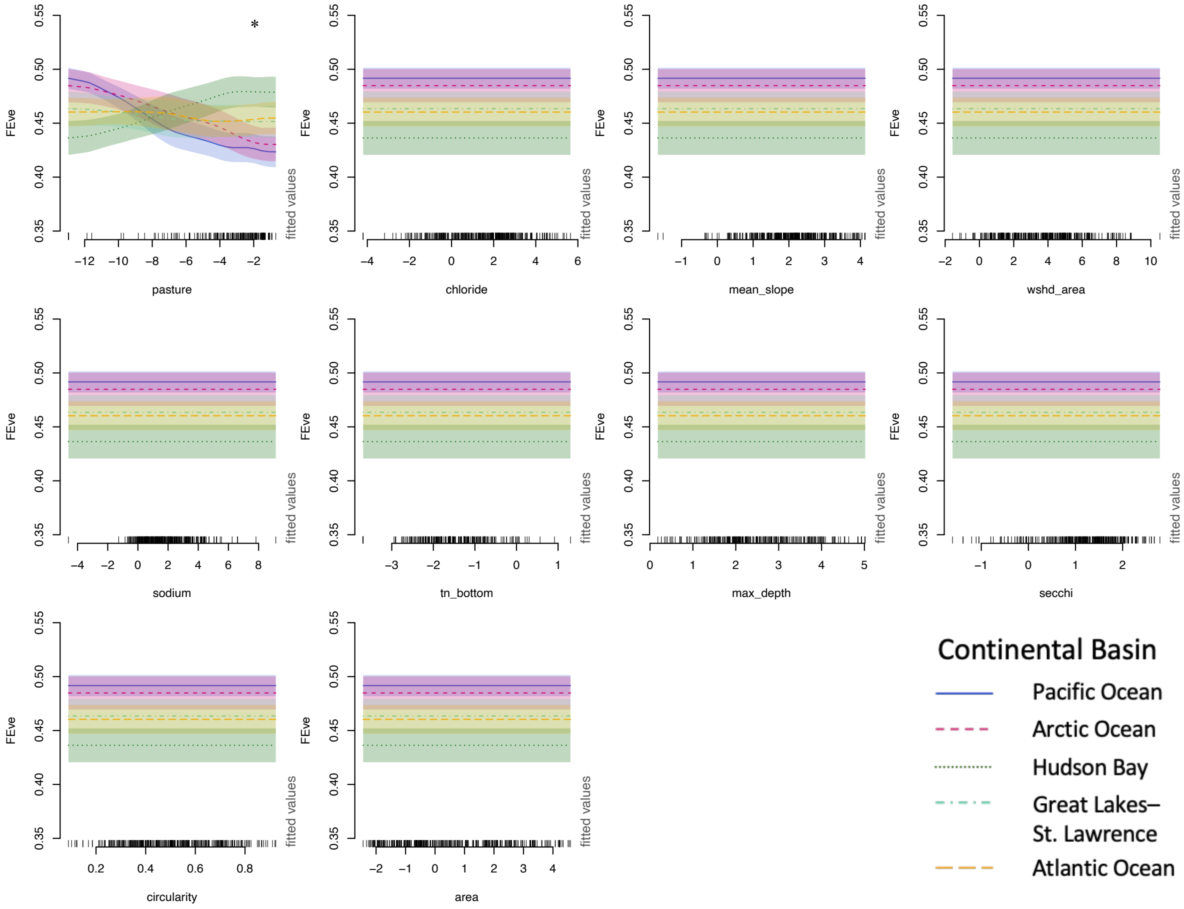
d) Richness


Richness
fitted values
***
circularity
0.2
0.4
0.6
0.8
**
planktivores
1.0
1.5
2.0
2.5
3.0
3.5
4.0
***
mean_slope
−1
0
1
2
3
4
wshd_area
−2
0
2
4
6
8
10
*
forestry
−12
−10
−8
−6
−4
−2
temp_epi
14
16
18
20
22
24
26
*
slope_100m
0
1
2
3
area
−2
−1
0
1
2
3
4
piscivores
1.0
1.5
2.0
2.5
3.0
3.5
colour
−2
0
2
4
6
4
5
6
7
8
9
10
Continental Basin
Pacific Ocean
Arctic Ocean
Hudson Bay
Great Lakes–
St. Lawrence
Atlantic Ocean

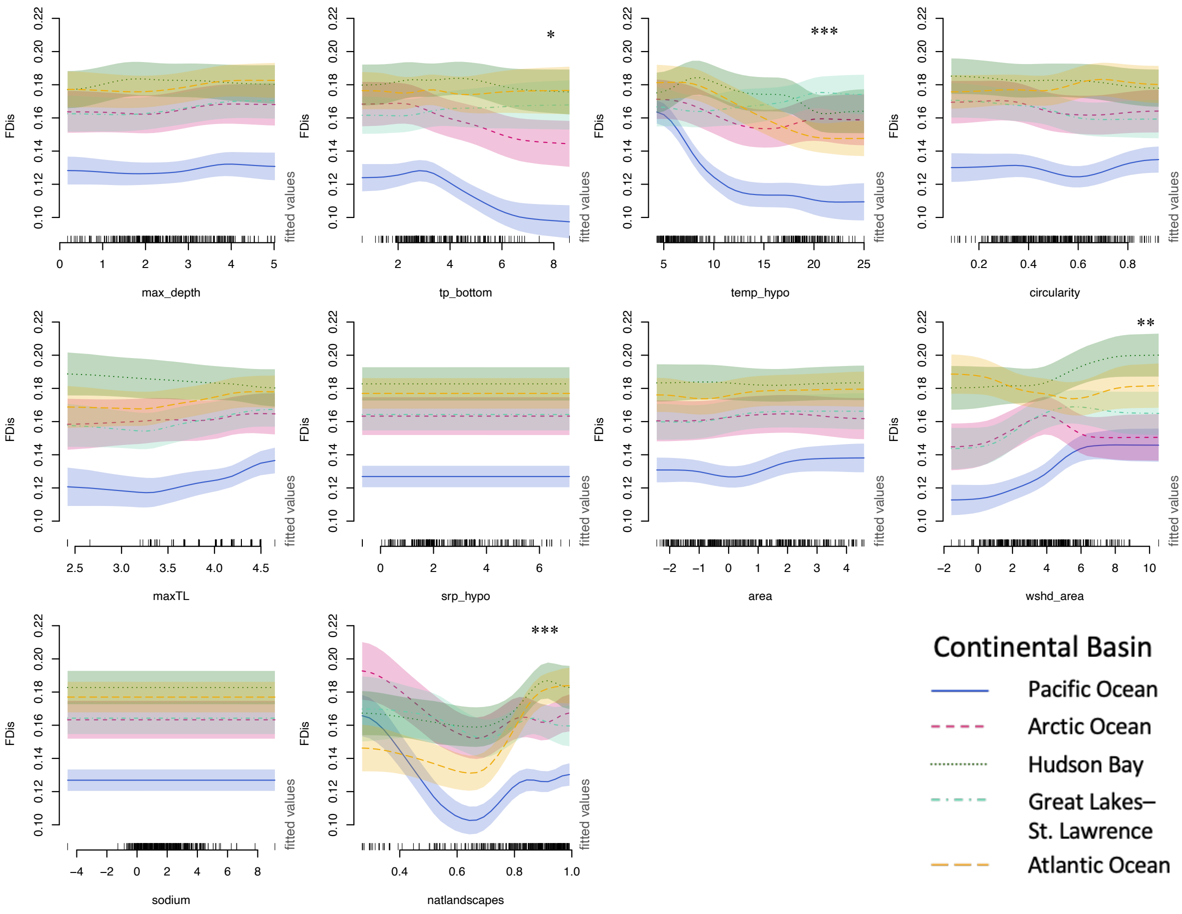
e) Rarefied richness



f) Functional evenness



g) Functional dispersion



h) Functional richness

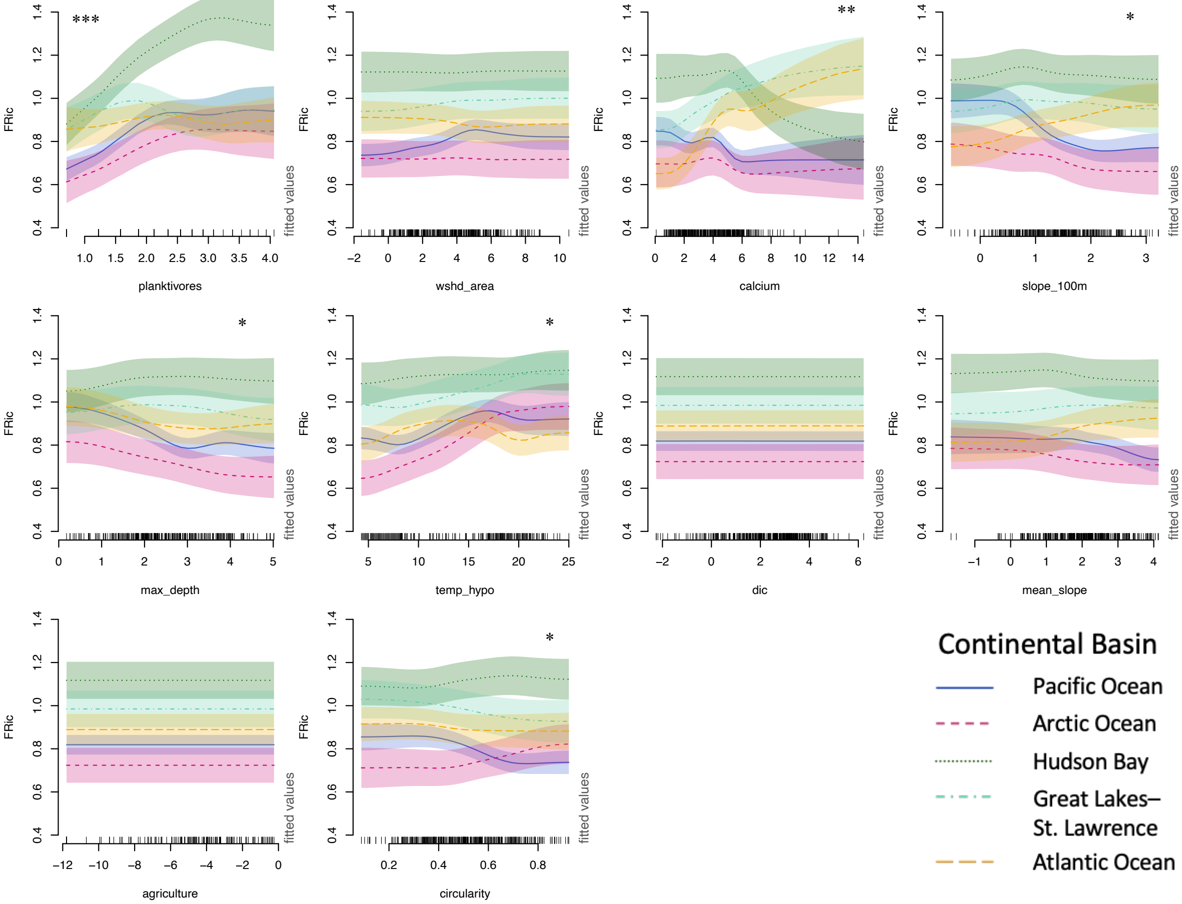
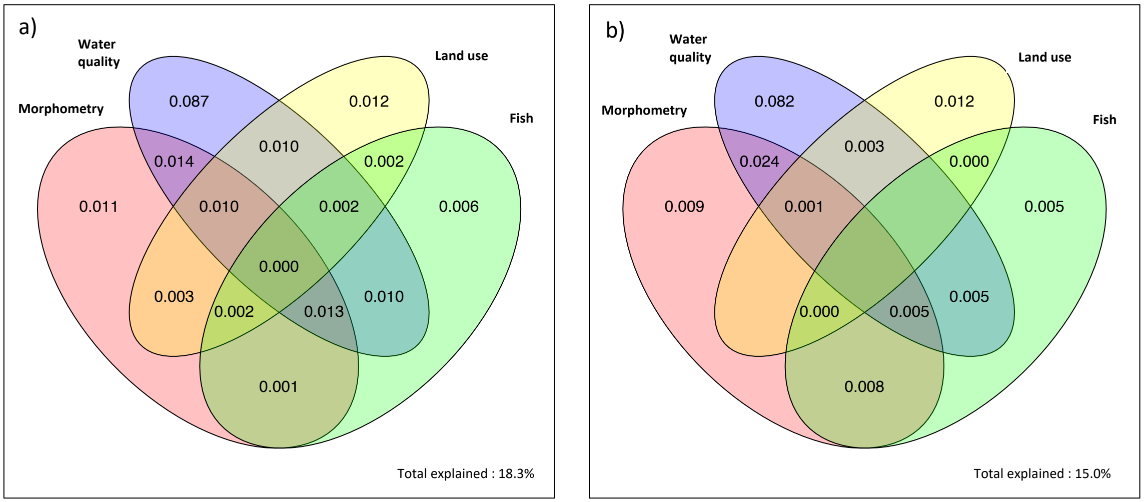


Figure L.1 General additive mixed model (GAMM) plots of fitted (a) Shannon diversity, (b) Simpson diversity, (c) Evenness, (d) richness, (e) rarefied richness, (f) functional evenness, (g) functional dispersion and (h) functional richness values against the ten most important predictors as sorted by Random Forest (RF) model, with continental basins as random smooth factor from the reduced 314 lakes dataset. Shaded area represents the confidence interval, reduced at se=0.5 to aid visualisation. *p-value<0.05; **p-value<0.01; ***p-value<0.001.

ANNEXE M

VARIATION PARTITIONING FOR THE 314 LAKES WITH FISH DATA, ACROSS ALL 624 CANADIAN LAKES, AND BY CONTINENTAL BASIN



Values <0 not shown

Figure M.1 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in the reduced 314 lakes where fish data was collected.

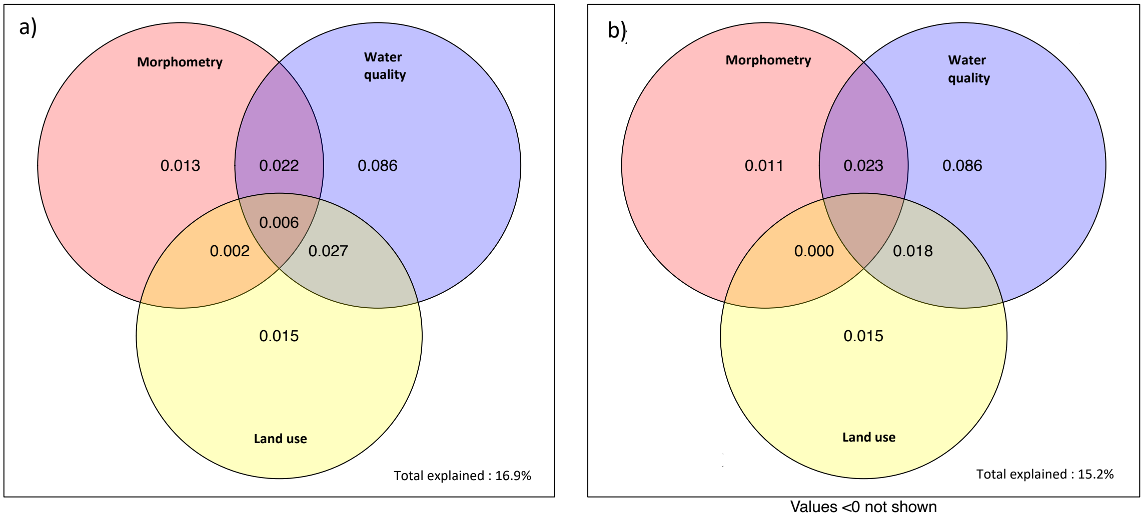


Figure M.2 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in across Canada.

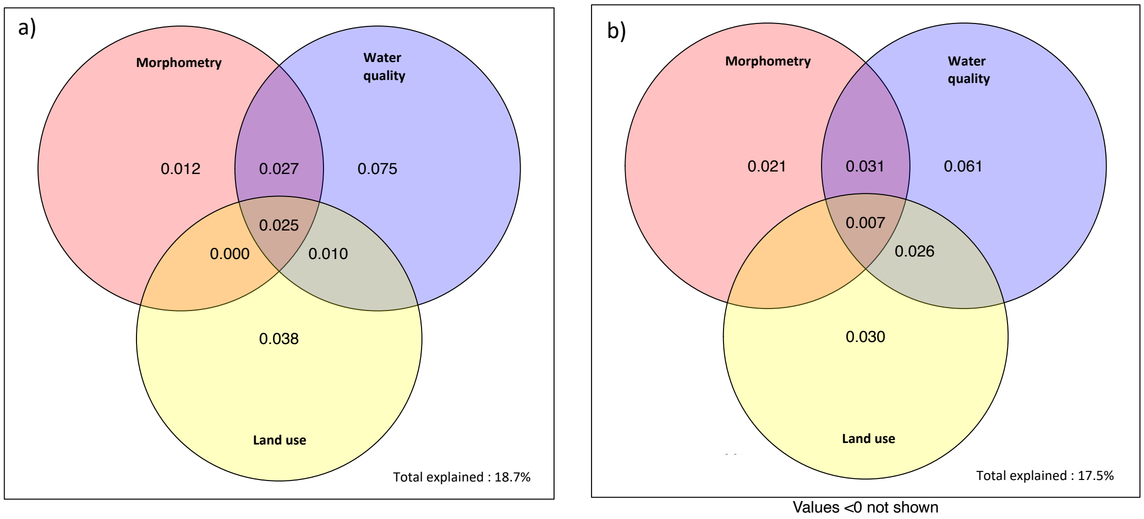


Figure M.3 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in the Pacific Ocean continental basin.

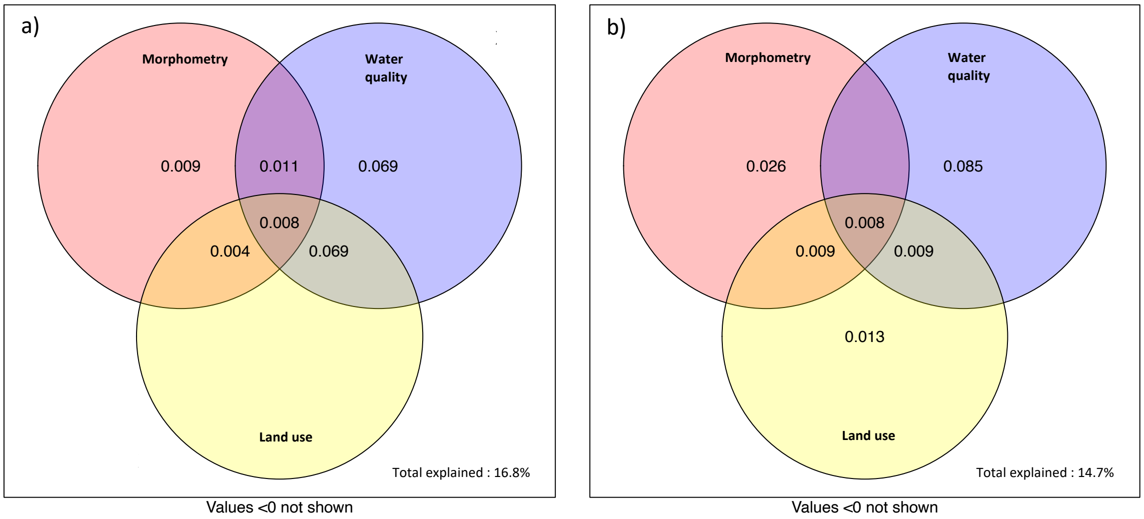


Figure M.4 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in the Arctic Ocean continental basin.

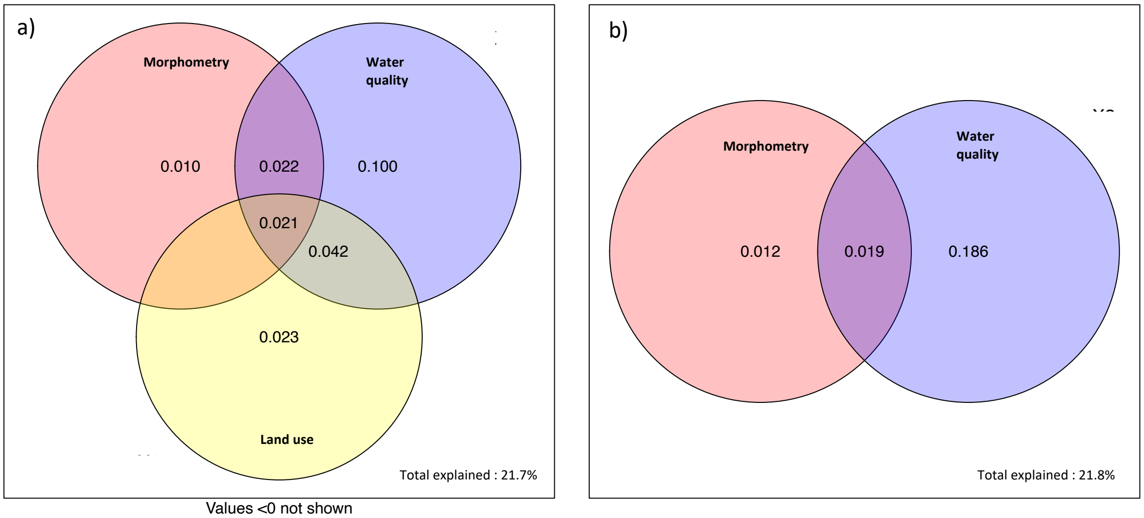


Figure M.5 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in the Hudson Bay continental basin.

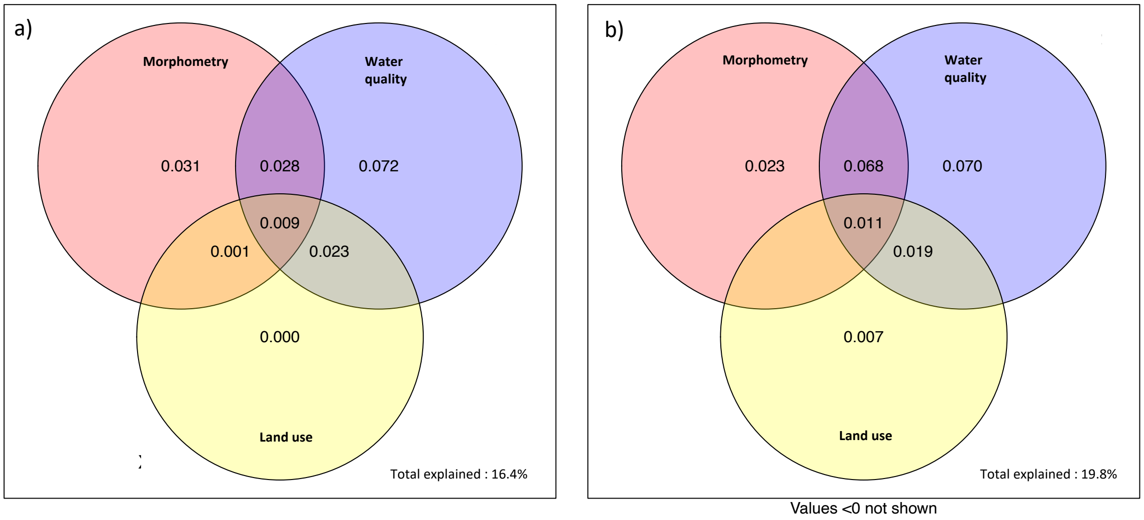


Figure M.6 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in the Great Lakes–St. Lawrence continental basin.

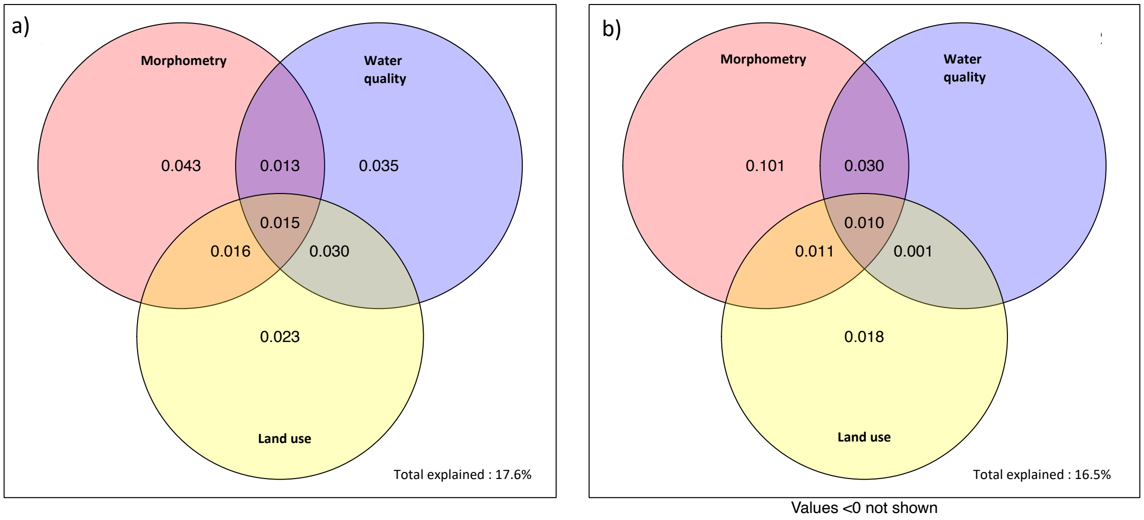


Figure M.7 Variation Partitioning for lake morphometry, water quality, land use and fish fractions for zooplankton taxonomic (a) and functional trait (b) community compositions in the Atlantic Ocean continental basin.

ANNEXE N

REDUNDANCY ANALYSES (RDA)

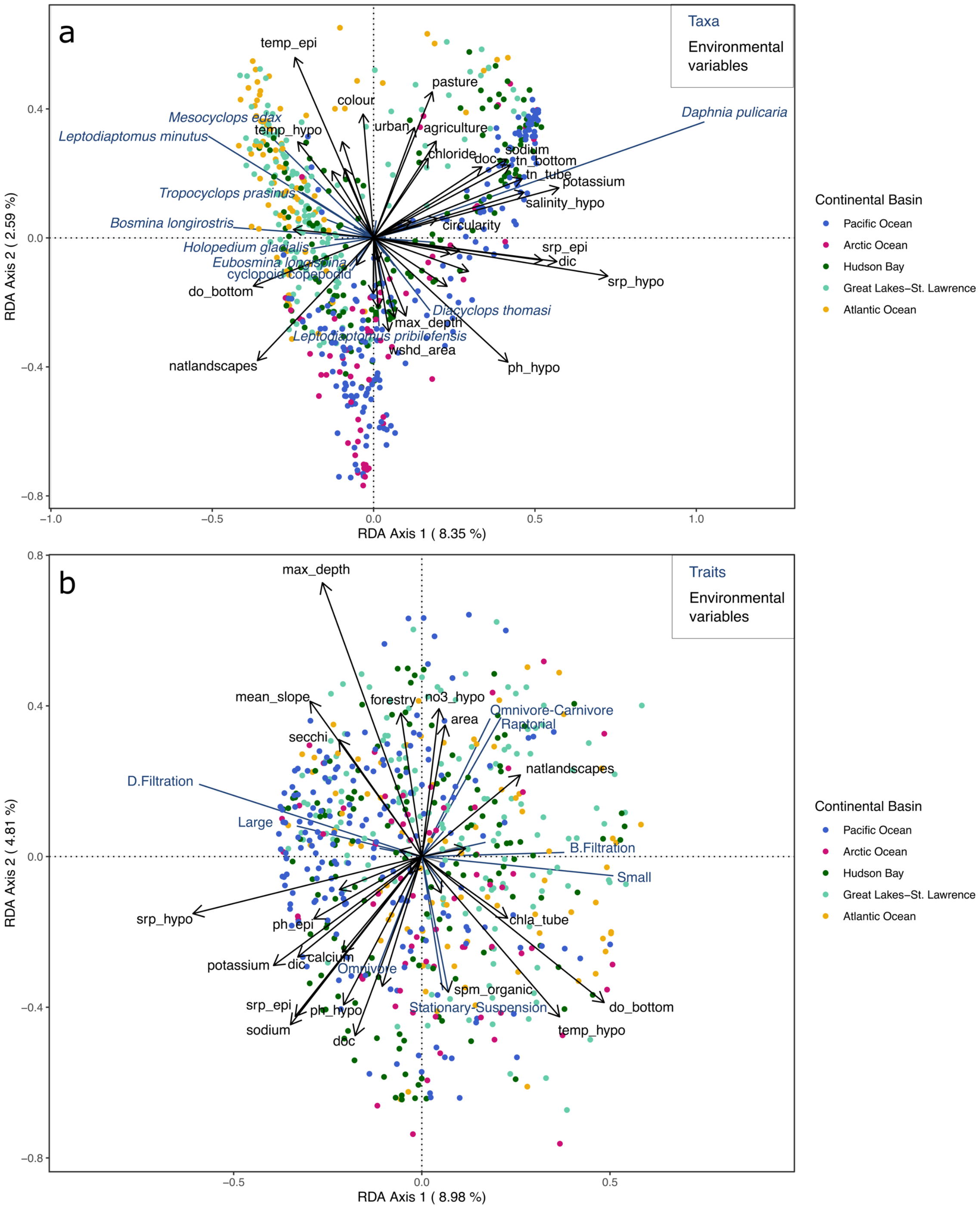


Figure N.1 Redundancy analyses (RDA) scaling 2 bi-plots of the taxonomic (a) and functional (b) zooplankton biomass from 624 sites (circles) colored by continental basin and constrained by forward-selected water quality, morphometric and land use variables.

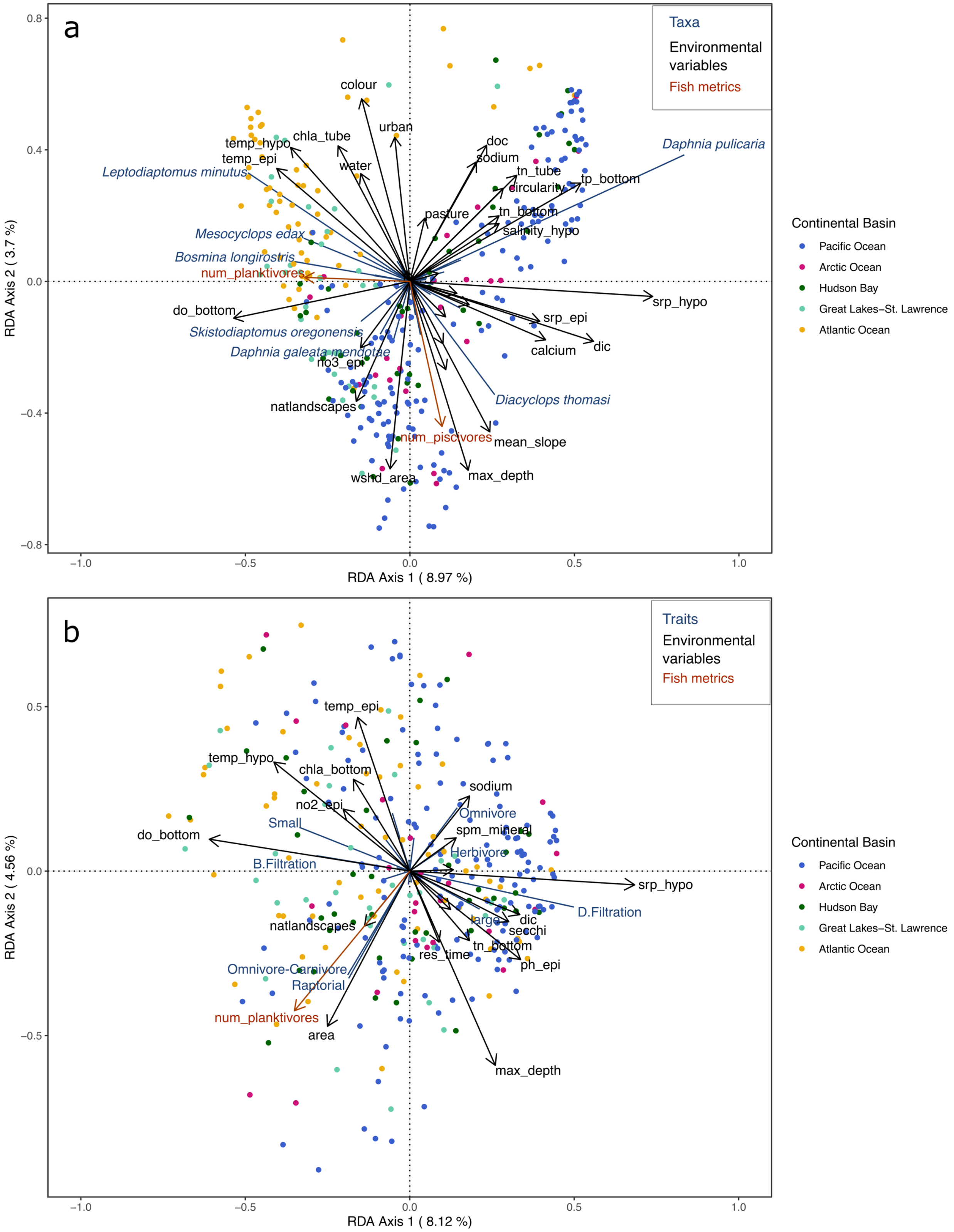


Figure N.2 Redundancy analyses (RDA) scaling 2 bi-plots of the taxonomic (a) and functional (b) zooplankton biomass from 314 sites with fish data (circles) colored by continental basin and constrained by forward-selected water quality, morphometric, land use and fish variables.

ANNEXE O

DATES OF PRE-INDUSTRIAL SAMPLES

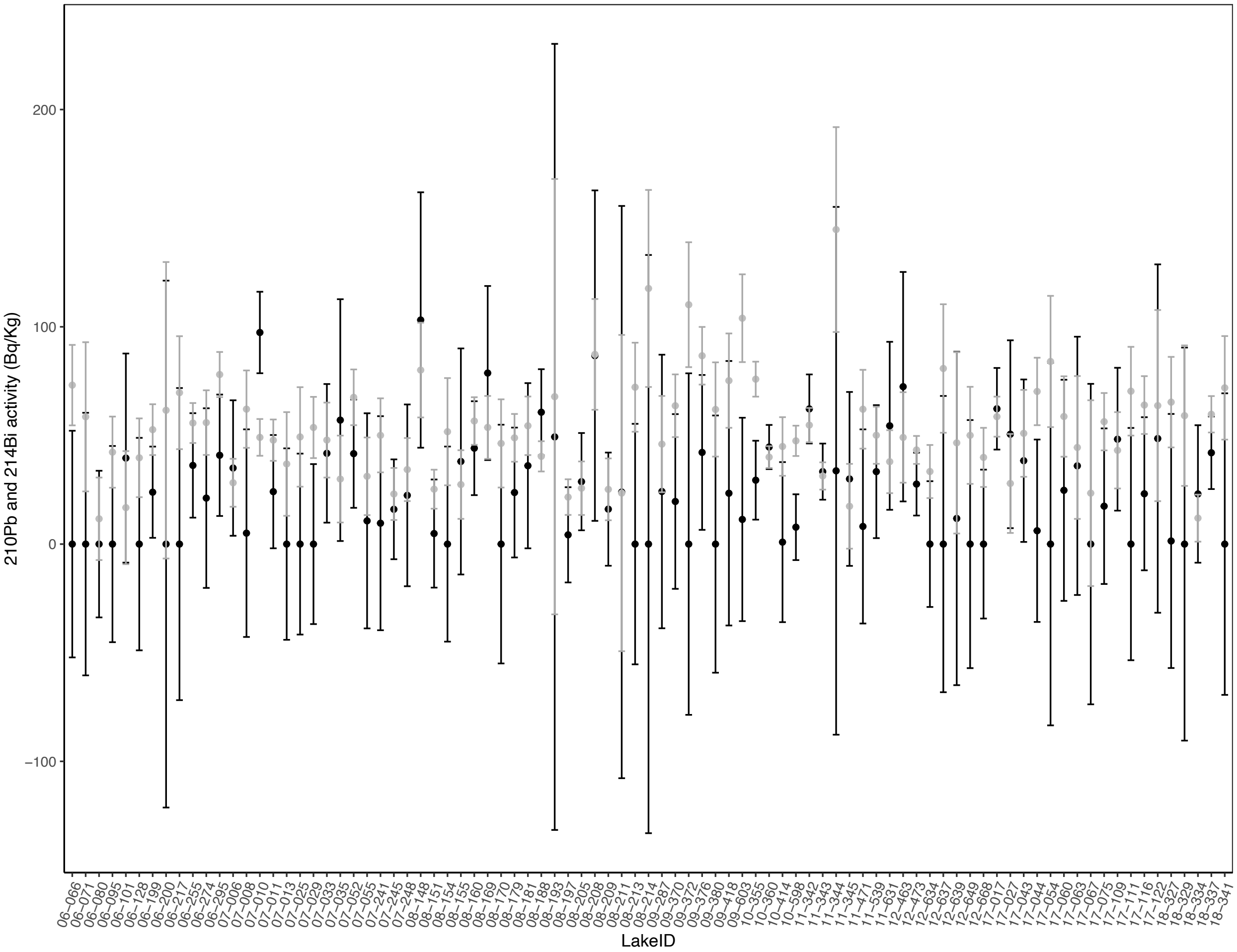


Figure O.1 ^{210}Pb (black) and ^{214}Bi activities (grey) of the bottom sediment of 87 cores analyzed within this paper. Bottom samples were considered pre-industrial when ^{210}Pb was below ^{214}Bi, including error bars. Only one core (07-010; low impact) did not reached background conditions.

ANNEXE P

SEDIMENTATION RATES AND DIVERSITY

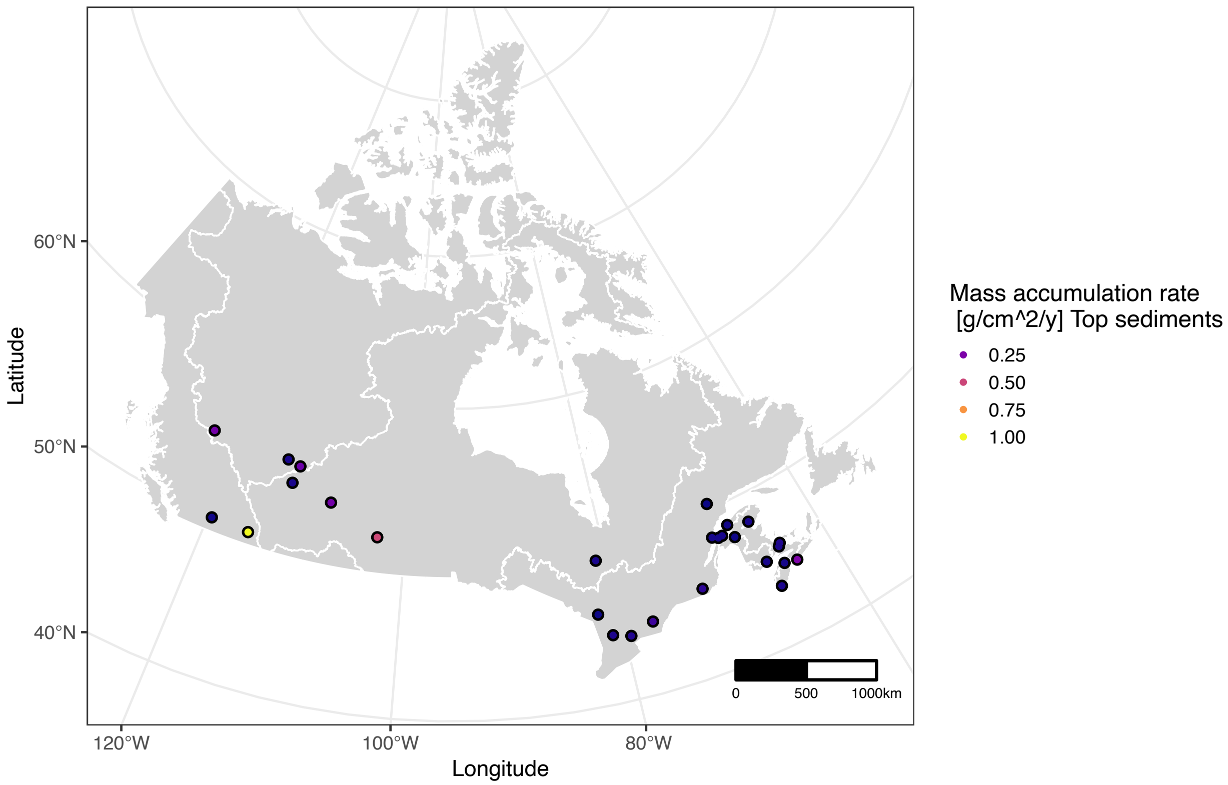


Figure P.1 Map of 27 sites selected for sediment rate estimations. Sites are contoured by continental basin and coloured by sediment mass accumulation rates in the top sediments. The map was created using Canada Atlas Lambert projection (NAD83 CSRS).

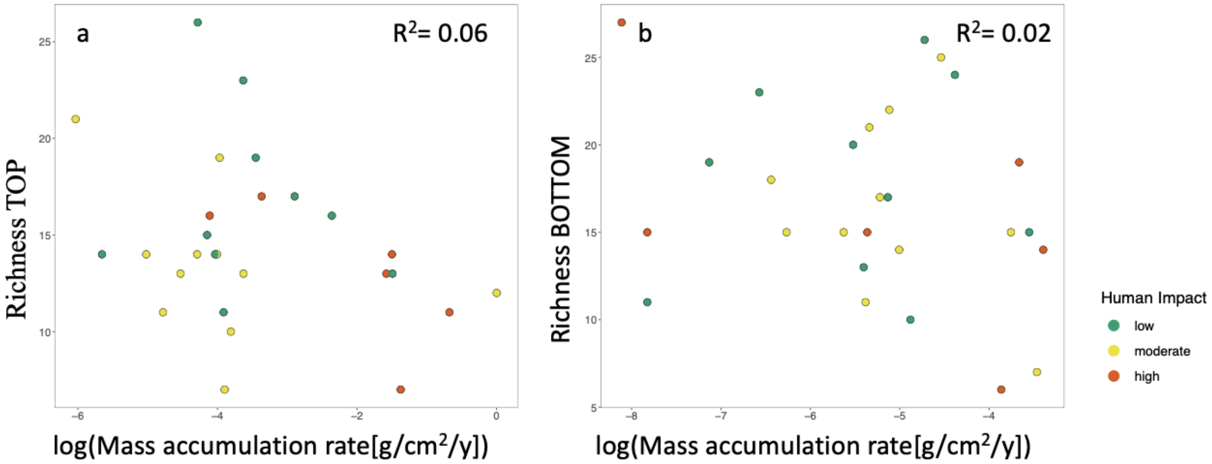


Figure P.2 Linear regression of species richness in the top (a) and bottom (b) sediments against log-transformed mass accumulation rates (g/cm2/year). Sedimentation rates were computed on full cores from 27 lakes collected at the same sampling location than cores for cladoceran analysis. Top accumulation rates are averages from the surface first centimeter of sediments. Bottom rates represent the deepest 1 cm interval where ^{210}Pb activity was detected. Note that the bottom depth of cladoceran samples were typically deeper that the bottom depth used for sediment rates estimations. We applied the constant rate supply (CRS) to calculate changes in sedimentation rates. Adjusted R-squared of linear models are displayed in each panel. Sites are coloured by human impact class. On average, the bottom 1 cm of the 27 dated full cores represented 3 times as many years as the top 1 cm interval (ranging from 0.2 to 18 times as many years), with the top 1 cm representing an average of 11 years of deposition (ranging from 0.6 years / cm to 49 years / cm) and the bottom 1 cm of the dated cores averaging 18 years of deposition (ranging from 1 to 45 years / cm). Error rates on the basal dates in a sediment core also typically increase with core depth, with an average error in on the top 1 cm date of 1 year (ranging from 0.03 to 5 years) and an average error on the bottom dated cm of 75 years (ranging from 2 to 933 years).

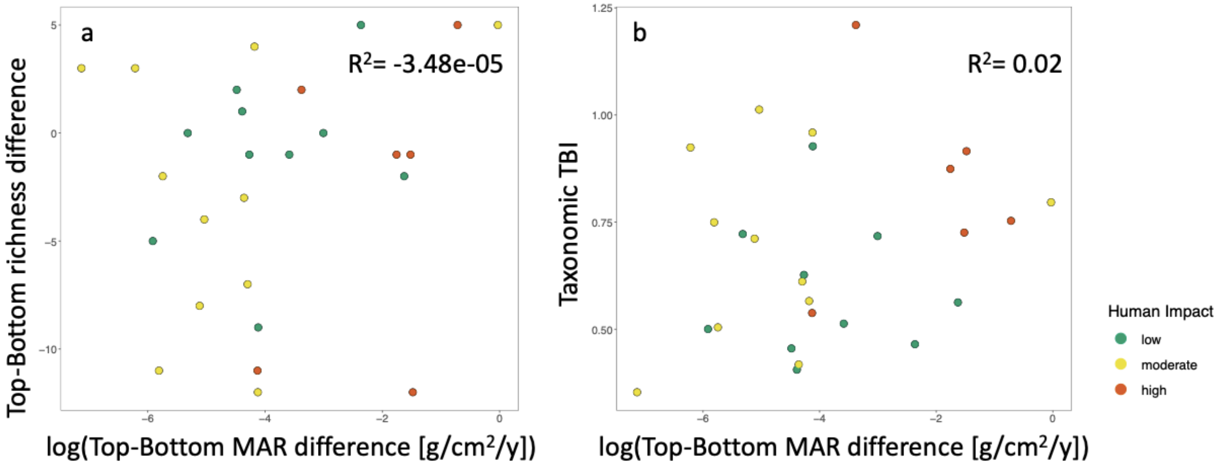


Figure P.3 Linear regression of species lost between bottom and top samples (a) and taxonomic temporal beta diversity (TBI; b) against log-transformed mass accumulation rates (g/cm2/year) between top and bottom samples. Sedimentation rates were computed on full cores from 27 lakes collected at the same sampling location than cores for cladoceran analysis. Top accumulation rates are averages from the surface first centimeter of sediments. Bottom rates represent the deepest 1 cm interval where ^{210}Pb activity was detected. Note that the bottom depth of cladoceran samples were typically deeper that the bottom depth used for sediment rates estimations. We applied the constant rate supply (CRS) to calculate changes in sedimentation rates. Adjusted R-squared of linear models are displayed in each panel. Sites are coloured by human impact class. On average, the bottom 1 cm of the 27 dated full cores represented 3 times as many years as the top 1 cm interval (ranging from 0.2 to 18 times as many years), with the top 1 cm representing an average of 11 years of deposition (ranging from 0.6 years / cm to 49 years / cm) and the bottom 1 cm of the dated cores averaging 18 years of deposition (ranging from 1 to 45 years / cm). Error rates on the basal dates in a sediment core also typically increase with core depth, with an average error in on the top 1 cm date of 1 year (ranging from 0.03 to 5 years) and an average error on the bottom dated cm of 75 years (ranging from 2 to 933 years).

ANNEXE Q

HUMAN IMPACT CLASSIFICATION

Table Q.1 Land use, human impact value, and data sources. Adapted from Huot *et al*., 2019.

Land Use	**Value**[1]	**Source**
Urban	1	Annual Space-Based Crop Inventory for Canada 2016 (Government of Canada, 2017); Land Use 2010 (Government of Canada, 2015); CanVec Manmade features 2017 (Government of Canada, 2018a)
Mines	1	CanVec Resources Management 2017 (Government of Canada, 2018b)
Agriculture	1	Annual Space-Based Crop Inventory for Canada 2016 (Government of Canada, 2017); Land Use 2010 (Government of Canada, 2015)
Pasture	0.5	Annual Space-Based Crop Inventory for Canada 2016 (Government of Canada, 2017); Land Use 2010 (Government of Canada, 2015)
Forest loss (last 5 years)	0.5	Year of gross forest cover loss event (2012 to 2016) (Hansen *et al*., 2013; World Resources Institute, n.d.)
Grassland Managed	0.3	Annual Space-Based Crop Inventory for Canada 2016 (Government of Canada, 2017); Land Use 2010 (Government of Canada, 2015)
Natural landscapes	0	Annual Space-Based Crop Inventory for Canada 2016 (Government of Canada, 2017); Land Use 2010 (Government of Canada, 2015)

[1]These values are attributed to each cell (30m*30m) of the land use raster layer.

References Annexe Q

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ANNEXE R

LOSSES AND GAINS

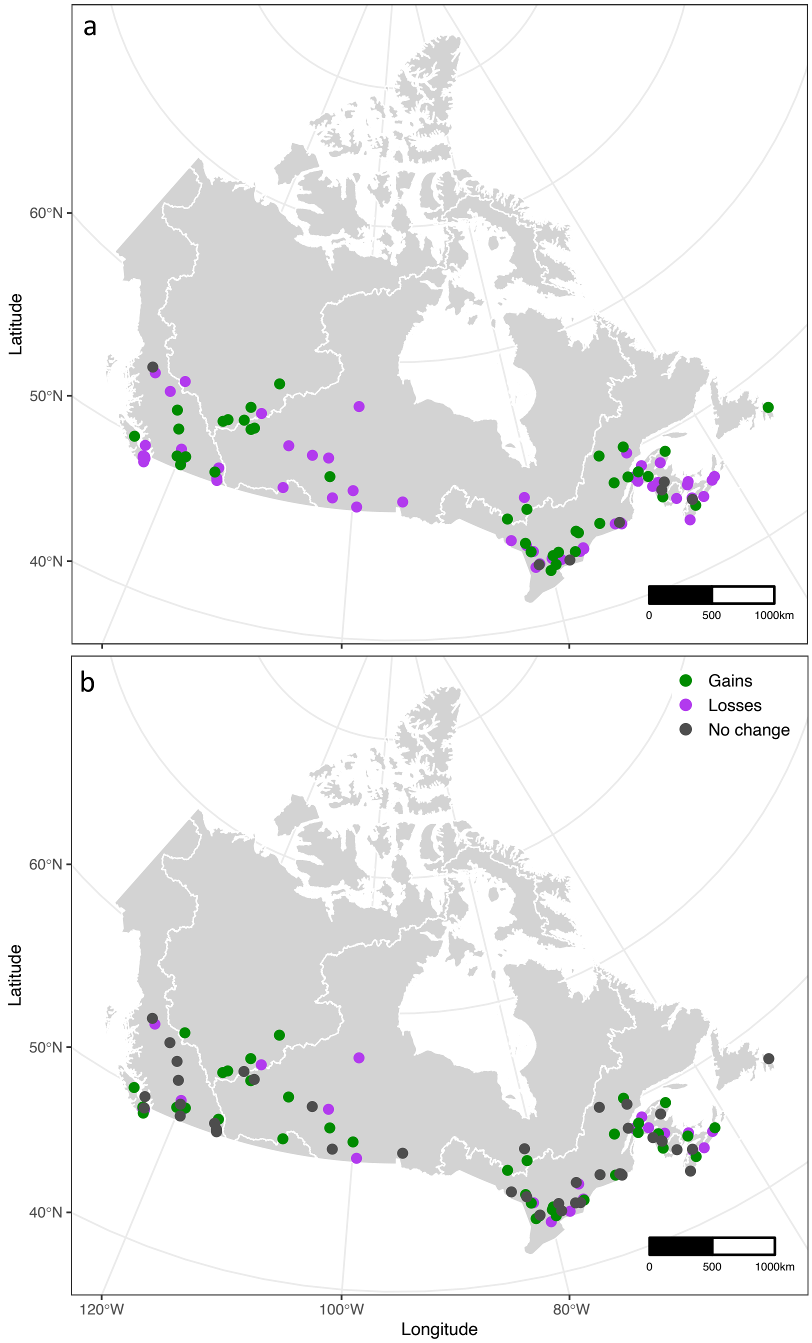

Figure R.1 Map of temporal taxa (a) or traits (b) losses or gains. Sites are contoured by continental basin and coloured temporal species change. The map was created using Canada Atlas Lambert projection (NAD83 CSRS).

ANNEXE S

SPATIAL AND TEMPORAL Β-DIVERSITY

Table S.1 Total taxonomic (a) and functional (b) β-diversity means by human impact. Pre-industrial and contemporary values are separated by an arrow when applicable. In bold are the largest values from each pairs. Significant p-values from the ANOVAs are shown.

a) **Human impact**	**Taxonomic Spatial β-diversity**	**Taxonomic temporal β-diversity**
All	0.33 -> **0.35**	0.65
Low	0.33-> **0.35**	0.60
Moderate	0.32-> **0.34**	0.67
High	0.34-> **0.35**	**0.72**
P-value	-	NS

b) **Human impact**	**Functional spatial β-diversity**	**Functional temporal β-diversity**
All	0.33 -> **0.35**	0.34
Low	**0.35**-> 0.34	0.33
Moderate	0.30-> **0.35**	0.33
High	0.33-> **0.35**	0.37
P-value	-	NS

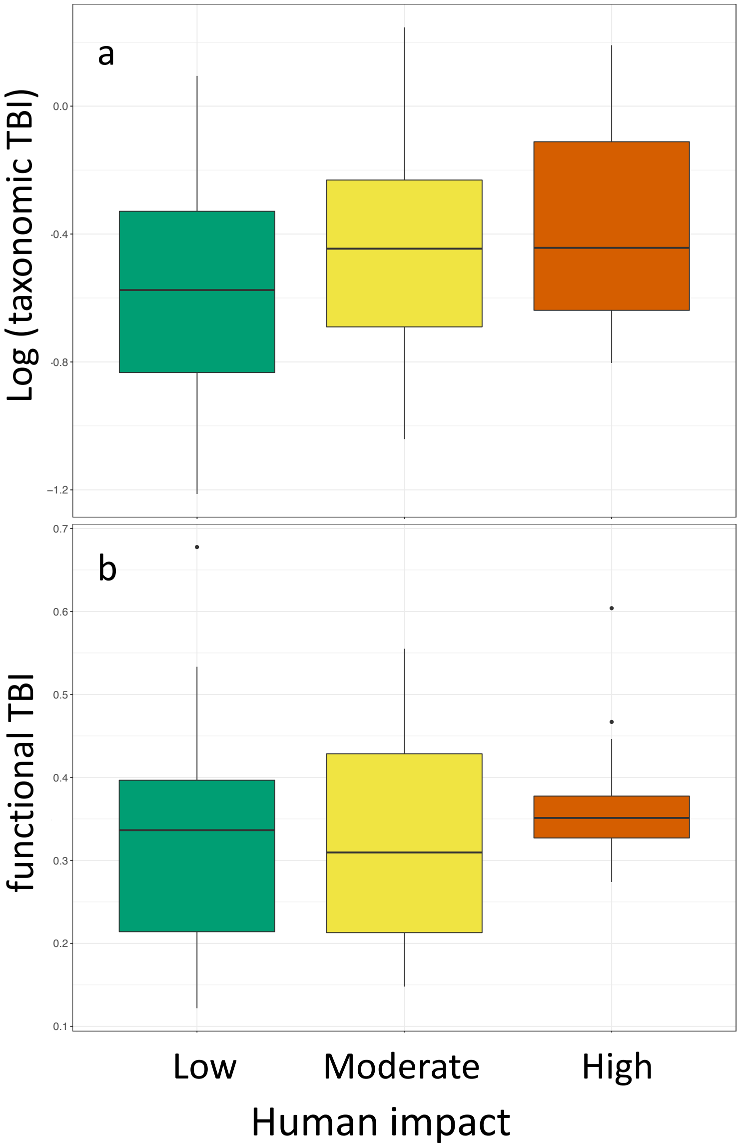

Figure S.1 Mean (± SE) of (a) taxonomic (log-transformed) and (b) functional temporal β-diversity values across human impact classes. Note that the y-axis scale varies between panels. There was no significant difference found between the human impact classes ($p>0.05$).

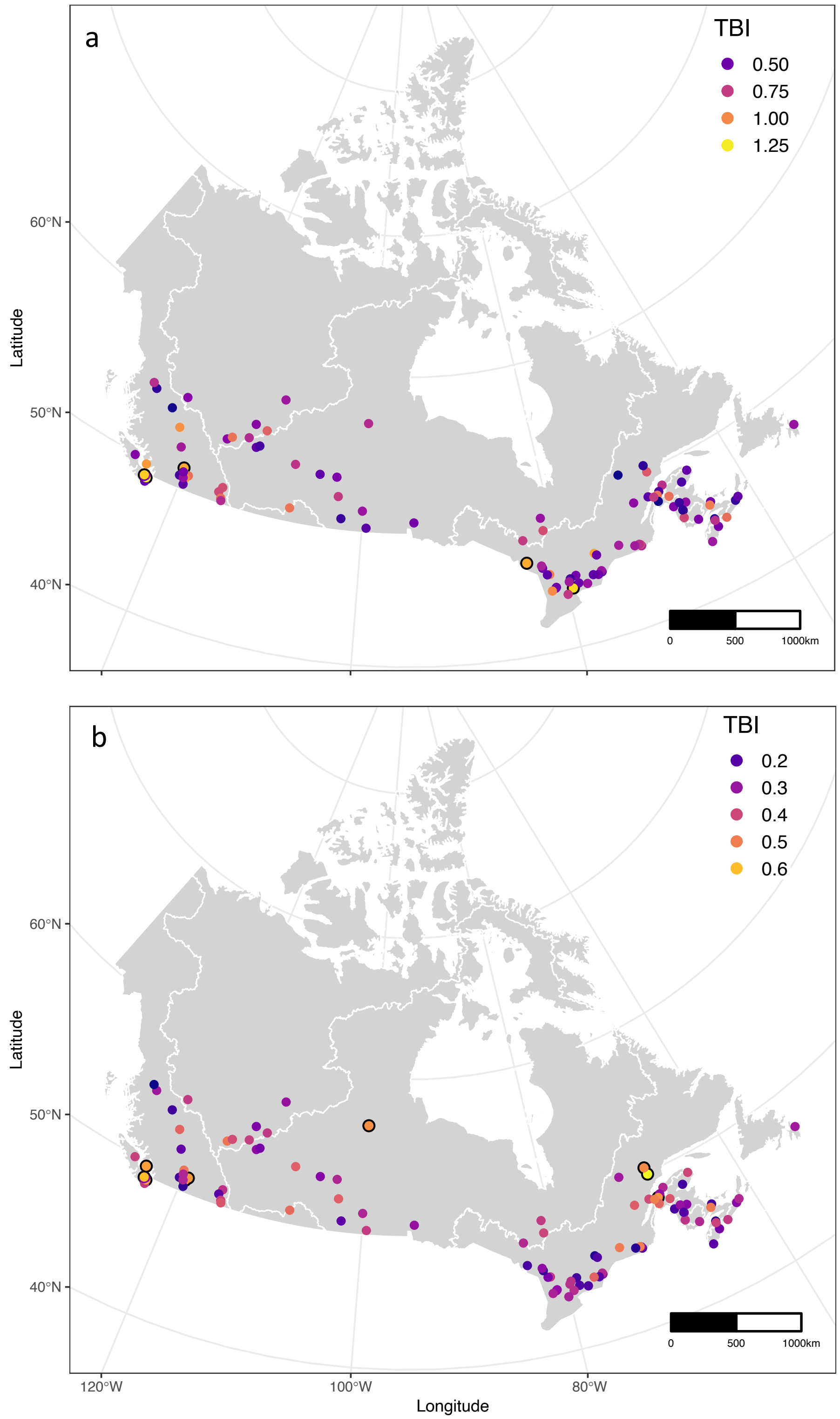

Figure S.2 Temporal taxonomic (a) and functional (b) β-diversity values across 101 Canadian lakes. Sites with significant exceptional lakes for the difference in species composition are contoured in black (a=5; b=9). The map was created using Canada Atlas Lambert projection (NAD83 CSRS).

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