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Diversité et structure du zooplancton: importance pour la conservation de la biodiversité aquatique en zone urbaine

par

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Résumé

L'écologie urbaine est un nouveau champ de recherche qui cherche à comprendre les structures et les patrons des communautés et des écosystèmes situés dans des paysages urbains. Les petits plans d'eau sont connus comme des écosystèmes aquatiques qui peuvent contenir une biodiversité considérable pour plusieurs groupes taxonomiques (oiseaux, amphibiens, macroinvertébrés), ce qui en fait des écosystèmes intéressants pour les études de conservation.

Cependant, la biodiversité du zooplancton, un élément central des réseaux trophiques aquatiques, n'est pas entièrement connue pour les plans d'eaux urbains et devrait être mieux décrite et comprise. Cette étude a évalué les patrons de biodiversité des communautés zooplanctoniques dans des plans d'eau urbains sur l'Ile de Montréal et leurs sources de variation. Des suggestions pour l'évaluation et la conservation de la biodiversité sont aussi discutées.

La biodiversité zooplanctonique des plans d'eaux urbains s'est avérée être assez élevée, avec les cladocères et les rotifères montrant les contributions à la diversité gamma et bêta les plus élevées. Sur l'ensemble des plans d'eau, il y avait une corrélation négative entre les contributions à la bêta diversité des cladocères et des rotifères. Au niveau de chaque plan d'eau, la zone littorale colonisée par des macrophytes s'est avérée être un habitat important pour la biodiversité zooplactonique, contribuant considérablement à la richesse en taxons, souvent avec une différente composition en espèces. Les communautés zooplanctoniques répondaient aux facteurs ascendants et descendants, mais aussi aux pratiques d'entretien, car le fait de vider les plans d'eau en hiver affecte la composition des communautés zooplanctoniques.

Les communautés de cladocères dans ces plans d'eau possédaient des quantités variables de diversité phylogénétique, ce qui permet de les classer afin de prioriser les sites à préserver par rapport à la diversité phylogénétique. Le choix des sites à préserver afin de maximiser la diversité phylogénétique devrait être correctement établi, afin d'eviter de faire des choix sous-optimaux. Cependant, pour des taxons tels que les cladocères, pour lesquels les relations phylogénétiques demeurent difficiles à établir, placer une confiance absolue dans un seul arbre est une procédure dangereuse. L'incorporation de l'incertitude phylogénétique a démontré que, lorsqu'elle est prise en compte, plusieurs différences potentielles entre la diversité phylogenétique ne sont plus supportées.

Les patrons de composition des communautés différaient entre les plans d'eau, les mois et les zones d'échantillonnage. Etant donné les intéractions sont significatives entres ces facters; ceci indique que tous ces facteurs devraient êtres considérés. L'urbanisation ne semblait pas sélectionner pour un type unique de composition des groupes alimentaires, étant donné que les communautés pouvaient changer entres des assemblages de types alimentaires différents. Les variables environnementales, surtout la couverture du plan d'eau en macrophytes, étaient des facteurs importants pour la biodiversité zooplanctonique, affectant la richesse spécifique de divers groupes taxonomiques et alimentaires. Ces variables affectaient aussi la composition des communautés, mais dans une moindre mesure, étant des variables explicatives modestes, ce qui indiquerait le besoin de considérer d'autres processus.

Mots-clés: Biodiversité, zooplancton, structure des communautés, écologie urbaine, zone littorale, diversité phylogénétique, héritage évolutionnaire, incertitude phylogénétique, préservation de sites, divérsité des cladocères, plans d'eau urbains, richesse spécifique, groupes alimentaires, gestion de la conservation

Abstract

Urban ecology is an emerging research field that seeks to understand the structures and patterns of communities and ecosystems located in urban landscapes. Small waterbodies are known as aquatic ecosystems that can harbour notable biodiversity for various taxonomic groups (birds, amphibians, macroinvertebrates), making them interesting ecosystems for conservation studies.

However, the biodiversity of zooplankton, a central element of aquatic trophic networks, is still not entirely known for urban waterbodies and should be better described and understood. This study examined the biodiversity patterns of zooplanktonic communities in urban waterbodies on the Island of Montreal and their sources of variation. Suggestions for biodiversity assessment and for biodiversity preservation are also discussed.

Zooplankton biodiversity urban waterbodies proved to be quite high, with cladoceran and rotifer taxa showing the highest contributions to gamma and beta diversity. Across waterbodies, there was a negative correlation between the contributions to cladoceran and rotifer beta diversity. Within waterbodies, the littoral zone showing macrophytes proved to be an important habitat for zooplankton biodiversity, considerably contributing species richness, often with a different species composition. Zooplankton communities responded to bottom-up and top-down forces, but also management practices, as waterbody emptying in winter affected zooplankton community composition.

Cladoceran communities in these waterbodies showed varying amounts of phylogenetic diversity, which allowed them to be ranked in order to prioritize sites to preserve with regards to phylogenetic diversity. Selection of sites to preserve in order to maximize phylogenetic diversity should be properly guided, in order to avoid making suboptimal

choices. However, for taxa such as Cladocera, for which phylogenetic relationships remain difficult to establish, placing absolute confidence in a single tree is a dangerous procedure. Incorporation of phylogenetic uncertainty showed that, when it is taken into account, then several potential differences in phylogenetic diversity were not supported anymore.

Community composition patterns differed between waterbodies, months and sampling zones. Due to the presence of significant interactions between these factors, this indicates that all these factors should be considered. Urbanization did not seem to select for a single type of feeding group composition, as communities in waterbodies could shift between assemblages with different feeding types. Environmental variables, especially waterbody macrophyte coverage, were important factors for zooplankton biodiversity, positively affected species richness of various taxonomic groups and feeding groups. These variables also affected community composition, but to a lesser extent, being modest predictor variables, indicating the need to consider other processes.

Keywords: Biodiversity, zooplankton, community structure, urban ecology, littoral zone, phylogenetic diversity, evolutionary heritage, phylogenetic uncertainty, site conservation, cladoceran diversity, urban waterbodies, species richness, feeding groups, conservation management

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ANOVA: Analysis of variance

cm: Centimetre

m: Metre

m²: Square metre

mL: Millilitre

L: Litre

LCBD: Local contribution to beta diversity

log$_e$: Natural logarithm

MANOVA: Multivariate analysis of variance

MCC: Maximum clade credibility

mtDNA: Mitochondrial DNA

NA: Not available

PD: Phylogenetic diversity

r: Pearson's correlation coefficient

R^2$_{adj}$: Adjusted coefficient of multiple determination

RDA: Redundancy analysis

SCBD: Species contribution to beta diversity

SE: Standard error

TP: Total phosphorus

µg: Microgram

µm: Micrometer

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Chapter 1

Introduction

1.1 Freshwater and its biodiversity

Water is an important and essential resource for human populations. Close to three quarters of the Earth's surface is covered by water, with most of it being from the World Ocean (Shiklomanov and Rodda 2003, Kotwicki 2009). The Earth's water reserves are estimated to be around 1 386 million km^3 of water (Shiklomanov 2000). However water resources are rather unevenly distributed between different compartments as although this number is high, fresh water represents only a small fraction of the world's water reserves. It is estimated that approximately 97.5% of the Earth's water is made up of saltwater (Shiklomanov 2000). Furthermore, even within the freshwater compartment, about two thirds of this water is locked in glaciers and ice caps and another third is made up of groundwater. This means other forms of fresh water, such as those that make up lakes, rivers and other freshwater ecosystems constitute less than 0.01% of the world's freshwater resources. Consequently, fresh water that is directly available to human exploitation and use represents only a very small fraction of the Earth's water reserves.

Water quality, use and management are pressing socio-economic and ecological issues that need to be addressed (Kuylenstierna et al. 1997, Gleick 1998, Johnson et al. 2001, Baron et al. 2002, Brooks and Brandes 2011). In addition to sources of water for drinking or sanitary purposes, freshwater ecosystems are also, among others, sources of irrigation water for agriculture, goods such as food and materials, hydroelectric power generation, as well as of recreation opportunities (Postel and Carpenter 1997, Wilson and Carpenter 1999). Furthermore, freshwater ecosystems also play important roles in the water cycle, as well as in several other important biogeochemical cycles including the carbon cycle, phosphorus and nitrogen cycle. Consequently, despite representing a small fraction of the world's water

compartments, freshwater ecosystems constitute an indispensable resource for both the viability of human populations as well as a variety of ecological processes.

Additionally, freshwater ecosystems constitute important habitats that contain important amounts of biodiversity. Currently, freshwater animals represent approximately 126 000 species, or around 9.5% of the total number of animal species recognized globally (Balian et al. 2008). The number of freshwater vertebrate taxa is quite high and includes at least 12 740 fish, 4 294 amphibian, 567 bird and 124 mammal species. Together, freshwater vertebrates represent up to 35% of all described vertebrate species. However, vertebrates make up only a small portion (14.5%) of known freshwater biodiversity. The major portion of freshwater diversity is made up of invertebrate taxa that contribute notably more to it. Invertebrates consist of an extremely diverse group of animals, which are linked by the fact that they do not possess a backbone. Together, freshwater invertebrates make up to 107 295 described species (Balian et al. 2008). These values are most certainly underestimates of the actual diversity of freshwater ecosystems. Indeed, current knowledge of freshwater biodiversity is incomplete and its estimation is a work in progress. For several taxonomic groups, the number of described species has considerably increased over the years (Balian et al. 2010). Increased sampling and study in lesser-known regions, as well as taxonomic re-evaluations of more difficult taxa will most surely increase the number of freshwater species (Lévêque et al. 2005, Dudgeon et al. 2006, Balian et al. 2008). Consequently, despite representing a small fraction of the world's water compartments, freshwater ecosystems contain considerable amount of diversity, making them important targets for conservation studies.

Freshwater ecosystems are heavily threatened by several factors which are linked with demand for their resources and increases in the human population. They face a number of threats such as organic pollution, habitat degradation and fragmentation, invasive species, increased water withdrawal and overexploitation of their resources. All of these have profoundly altered various physical, chemical and biological aspects of freshwater ecosystems (Carpenter et al. 2011). Consequently, several of the world's freshwater ecosystems are noticeably modified by anthropogenic activities and pressures that also threaten freshwater biodiversity, leading several species to vulnerable or endangered status (Dudgeon et al. 2006, Darwall et al. 2009). Pronounced losses can be expected and projected extinction rates for North American freshwater fauna are as high as those in tropical forests, one of the world's most endangered biomes (Ricciardi and Rasmussen 1999). Therefore, unless action is undertaken to better study and preserve these ecosystems, the resources and services they offer will be lost. This would call for increased awareness of freshwater biodiversity and its value, as well as the development and implementation of biodiversity conservation plans to prevent further biodiversity loss.

1.2 The importance of small waterbodies

Much of the interest in freshwater studies has concentrated on relatively large lakes and rivers. Relative to the interest that these ecosystems have garnered, other freshwater habitats such as ponds and other small waterbodies have not had the same degree of attention. However, small lakes and ponds are quite common, and recent estimates show that they may be extremely numerous (Downing et al. 2006), with these values being reevaluated through theoretical (Seekell and Pace 2011) and empirical studies (McDonald et al. 2012). They are

now considered to be important ecosystems that play out a role in water balance, sedimentation and the carbon cycle (Downing et al. 2008, Downing 2010). Consequently, despite their smaller size, small lakes and ponds are underappreciated aquatic environments that should be included in research studies to obtain a better understanding of freshwater ecological patterns and processes.

Scientific interest in the biodiversity of these small waterbodies has also increased considerably over the last years (Oertli et al. 2009). This increase can be attributed to the fact that these small waterbodies represent important biological habitats that harbour substantial biodiversity. Indeed, ponds have been noted to contain several species labelled as rare or unique and can contribute noticeably to landscape diversity (Oertli et al. 2002, Williams et al. 2003, Wood et al. 2003). This high biodiversity can be the result of the heterogeneity in environmental conditions among these waterbodies, as they can vary considerably in terms of shapes, sizes, hydroperiod, and water quality, among others. The often large amount of heterogeneity displayed by ponds, along with their high numbers should create a wide array of habitats for various communities to develop, as well as to promote landscape biodiversity. Furthermore, ponds also represent key ecosystems that are especially amenable to the testing of ecological and evolutionary hypotheses (De Meester et al. 2005). Consequently, as we increase our knowledge of pond ecology, we also gain a deeper appreciation of the scientific resource and value they represent.

Despite this growing interest, increasing pressure owing to urban encroachment and agricultural intensification have led to a considerable decline in aquatic habitat numbers in many areas (Wood et al. 2003, Hassall 2014). Furthermore, affected waterbodies face a number of threats, such as increased pollution in organic contaminants and heavy metals,

changes in their trophic state and pH, habitat loss due to changes in land use, invasive species and global change (Brönmark and Hansson 2002, E.P.C.N. 2007, 2008). Additionally, ponds and small waterbodies are somewhat inadequately protected due to their small size which, with very few exceptions, excludes them from formal protection plans (Nicolet et al. 2007, E.P.C.N. 2008, Miracle et al. 2010, Möckel 2013, Hassall 2014). Furthermore, for waterbodies located in urban environments, human population density and the ensuing anthropogenic stressors may also have strong impacts. In these cases, inappropriate management of waterbodies or their surrounding environment can affect the communities they harbour.

Consequently, although they can be very numerous, contribute to important ecological processes and have the potential to harbour substantial amounts of biodiversity, ponds and other small waterbodies are amongst the least well-protected and least well understood freshwater ecosystems. Pond conservation can be carried out through various legislation and national efforts, but there is a need to study them further, as well as to develop conservation strategies directly for them. Efforts have been carried out to study, promote and preserve their biodiversity (Biggs et al. 1991, Biggs et al. 2005, Oertli et al. 2005b, E.P.C.N. 2007, 2008, Céréghino et al. 2008). However, this accumulation of knowledge is a work in progress and further scientific knowledge is needed, especially in the case of urban waterbodies. Further knowledge regarding species distribution patterns and their sources of variation is necessary to be able to properly evaluate their biodiversity potential, as well as to manage and preserve these habitats and their communities.

1.3 Human interactions with waterbodies

Human interactions with ponds and small waterbodies are varied and have existed for quite a long time. The diverse relationship between man and ponds is seen in the countless functions and uses that they may derive from them (Rees 1997, E.P.C.N. 2008, Hassall 2014). Over time, humans have used ponds for several purposes, including as sources of food and drinking water, but also for more complex and elaborate uses such as irrigation ponds for agriculture, watering ponds for livestock, retention and sedimentation ponds, or ponds for a variety of industrial processes. These many uses of ponds by humans give them an amenity value and, in some cases, economic profit can be gained from the exploitation of their resources. Furthermore, these waterbodies have also been integrated as part of some societies' culture and history. Consequently, these habitats also possess a social and cultural value, which should also be taken into account when assessing their value (Rees 1997, E.P.C.N. 2007, 2008, Boix et al. 2012). Waterbodies are therefore important elements of the local landscape that can share a deep bond with human society.

Furthermore, humans share an affective link with water, as the presence of water is usually perceived as a scenic, pleasant and aesthetic component that people usually enjoy. Humans often show preference towards certain kinds of waterbodies (Ulrich 1983, Herzog 1985, Bulut and Yilmaz 2009, White et al. 2010). Furthermore, aquatic environments can provide several benefits, affecting health and well-being, as well as serving as a place for recreational activities (Völker and Kistemann 2011, 2013). When this is the case, people want to have these waterbodies around them simply for the affectionate relationship they have with them and the therapeutic and aesthetic benefits they can draw from them. Likewise, another human-centric, but interesting, relationship between humans and waterbodies involves real

estate appreciation, wherein property values can be affected by the proximity to the waterbody (Doss and Taff 1996, Luttik 2000, Mahan et al. 2000, Cohen et al. 2014). Consequently, despite considerable declines in the number of small waterbodies due to increase in urban space and agricultural intensification, small waterbodies can still hold a place for human society. Their numbers and uses in human-dominated environments are likely to be related to changes in human's perception of them.

The presence of urban ecosystems means that they may provide ecosystem services, which can be both varied and important. These services are diverse and include direct use such as food and water sources, indirect uses such as noise reduction and water purification, as well as more psychological or emotional uses such as recreation, spirituality and population well-being (Bolund and Hunhammar 1999, Gómez-Baggethun and Barton 2013, Gómez-Baggethun et al. 2013). In the case of aquatic ecosystems, water treatment and the removal of contaminants and waste from the water by aquatic communities may be an interesting and less invasive practice to obtaining cleaner waters. Wetlands may reduce the amount of various elements such as nutrients, heavy metals and pesticides (Brix 1994a, Kohler et al. 2004, Rai 2008) that accumulate in urban waters. In addition to these services, ponds also may possess a social function, being sites where recreational activities such as swimming, fishing or gatherings can take place. Furthermore, their presence could also have therapeutic benefits that increase the health and well-being of people (Völker and Kistemann 2011, 2013, White et al. 2010). Finally, urban waterbodies may represent reservoirs of biodiversity in an urban environment. They may possess noticeable diversity in ecological communities, represent refuges for several animal species and, in some cases, they can contribute to regional

biodiversity (Hassall 2014). These diverse functions further enhance the potential that can be gained from proper management of urban aquatic ecosystems.

However, the amount, value and limits of these services need to be assessed, as they may vary between cities for socio-economic and cultural reasons. Furthermore, the notion of urban ecosystems and their biodiversity are not always synonymous with benefits to human society. Indeed, ecosystem disservices, or aspects of ecosystems that are perceived as negative by humans, can also come into play and should be considered (Lyytimäki et al. 2008, Lyytimäki and Sipilä 2009, Gómez-Baggethun and Barton 2013, Gómez-Baggethun et al. 2013). Disservices of aquatic ecosystems include negative water quality and harbouring waterborne pathogens and diseases when polluted. Ponds can also develop cyanobacteria blooms, whose toxins can pose serious health risks to humans and pets (Waajen et al. 2014). Aquatic environments may attract wild animals and pests, and the water can become a breeding ground for biting insects such as mosquitoes. Finally, when considering the construction and arrangement of ponds, the safety of certain people, especially children, must be considered (Baxter et al. 1985, Emery 1986, Danks 2001). Consequently, even though urban ponds can provide several ecosystem services, these ecosystem disservices should not be neglected as they are part of these habitats.

Finally, the biological, economic and cultural values we attribute to these waterbodies sometimes clash with each other, as they can lead to conflicting management strategies for waterbodies. For example, the use of plants to take up contaminants or nutrients may involve their removal. Macrophytes may also be removed for visual and aesthetic purposes or because they may be considered as weeds. However, such actions should take into consideration the ecological role that macrophytes play as, in addition to providing habitat for diverse aquatic

wildlife, macrophytes play out several ecological roles in wetlands (Brix 1994a, 1994b, 1997). Likewise, exotic species often have negative impacts on the ecosystems in which they are introduced. However, part of the appeal of certain ponds can also include the presence of exotic or nonnative species, sometimes which can even form part of the waterbody's history. If the historical value of these waterbodies is to be prioritized, then such macrophyte species must be considered as part of the ponds' landscape (Rees 1997). Finally, prioritization of the biological value of the waterbody's diversity could call for some waterbodies' amenity usage to be altered or stopped, thus having potential economic or social impacts.

Thus, it becomes clear that the issue of biodiversity and its conservation for waterbodies located within urban environments can be a difficult issue due to their complex relationship with humans and the various stakeholder types that may be involved. Conservation plans are charged with the difficult task of weighing these different values and making informed decisions. The advantages and disadvantages of specific decisions regarding waterbody management should be carefully considered before any action is undertaken. If poorly informed practices are undertaken, then urban ecosystems can become more of a nuisance than an asset and much of their value can be lost. Indeed, under informed maintenance of waterbodies, education of the public, and when biodiversity is promoted, many of the ecosystem disservices and conflicts related to waterbody usage can be resolved.

1.4 Importance of ponds for the conservation of urban biodiversity

The human population is becoming increasingly urbanized. More than half of the Earth's population lives in towns or cities (United Nations 2014). This trend is likely to increase, owing to several causes, including natural urban population increase, the annexation

and reclassification of land around the periphery as well as urban or rural-to-urban migration (Cohen 2004). By 2008, there were 19 megacities (cities with over 10 million inhabitants) in the world and as of 2015, there are currently 36 megacities in the world. Furthermore, there are over 500 agglomerations of over 1 million inhabitants (Brinkhoff 2003). However, urban population will continue to be distributed among urban areas of all sizes, including smaller population centers (Hardoy et al. 2001, Cohen 2004). Despite differing definitions of the term "urban" (McIntyre et al. 2000, Frey and Zimmer 2001, Cohen 2004), urbanization represents an important phenomenon for human society.

The presence of human populations and their associated activities have varied ecological effects on urban ecosystems and their associated biological communities. These effects can vary amongst taxonomic groups and land-use types (McKinney 2002, 2008, Alberti 2005). However, urban areas are not completely devoid of nature, as biodiversity can be seen in parks, ponds or even within unexpected places such as buildings, gardens or homes. These urban environments can be considerably different than more natural ones due to human presence and anthropogenic stressors, and they may also provide interesting ecological opportunities (Alberti et al. 2003, Alberti 2005, Kowarik 2011). Within urban ecosystems, biological communities may not be subjected to the same factors because of the presence of additional stressors not found in the natural environment.

Consequently, to obtain a better understanding of urban biodiversity patterns, as well as the structure and function of populations, communities and ecosystems in urban landscapes, these issues need to be taken into account (Pickett et al. 1997, Collins et al. 2000, Grimm et al. 2000, McDonnell and Hahs 2013). Urban waterbodies represent complex ecosystems that respond to various ecological factors and anthropic stressors, but also citizen's attitudes and

perception, which may affect their management and viability. Indeed, public perception of ecosystems and their willingness to change it can be a strong force that affects ecosystems, as landscapes valued for their appearance are more likely to exist over the long-term in a human-dominated landscape (Nassauer 1997, Décamps 2001, Robertson and Hull 2001, Nassauer 2004). In some cases, people can employ certain practices or modify certain aspects of these waterbodies, which may not always have positive consequences for aquatic biodiversity. Furthermore, as humanity is increasingly more urbanized and owing to their proximity to city centers and human stressors, studying urban waterbodies may be the most direct approach for assessing the effects of anthropogenic stressors on biodiversity and communities, as well as developing management policies favouring biodiversity conservation.

An invaluable element of any conservation evaluation plan is the knowledge of what kind of biodiversity there is, how much of it there is, where it is located and how it varies. However, even though urban pond communities have been the focus of a range of various studies (Hassall 2014), the amount and type of biodiversity that is present in urban waterbodies is still relatively unknown. Additionally, the role that these waterbodies play as potential reservoirs of urban biodiversity should be further evaluated. Indeed, it seems that they may play an important role in biodiversity conservation, as some studies have report considerable amounts of biodiversity in urban environments for various aquatic communities (Ejsmont-Karabin and Kuczyńska-Kippen 2001, Santoul et al. 2009, Vermonden et al. 2009). However, low ecological values have also been reported (Noble and Hassall 2014). Therefore, it could be that beyond a certain point of negative management, the biodiversity potential of urban ponds is lost, which means that a general role for these waterbodies could be difficult to establish.

Since they are part of the urban landscape, humans will often interact with waterbodies and can have expectations regarding their appearance. This and the possible affective relationship between waterbodies and human populations can have a number of implications for environmental planning and design. In urban environments, waterbodies may be modified, removed or created in response to particular societal demands. These can be completely different from the ecological demands of waterbodies. In the case of aquatic environments, people show preferences for different attributes, such as its size, the presence of macrophytes, water color, transparency, whether water is moving or not, as well as visual cues (Wilson et al. 1995, Wherrett 2000, Nasar and Lin 2003, Nasar and Minhui 2004, Cottet et al. 2013). City officials and park managers may seek this information in order to rearrange or design new waterbodies so as to make them more appealing, and increase the number of visitors or their well-being.

Though such practices can satisfy citizens and give them a higher degree of well-being, they may have several negative consequences for the ecology of urban waterbodies. Indeed, if only human design preference is followed, homogeneity of waterbodies can occur. Currently, citizen and manager preferences tend toward larger waterbodies, with well-kept vegetation, preferably oligotrophic and whose water could be treated in order to obtain cleaner and clearer waters (Biggs et al. 1994, Nassauer 2004, Hassall 2014). The loss of ecological diversity of habitats due to these practices should have detrimental effects on landscape biodiversity. It has been suggested that conservation policies should consider all waterbody size ranges (Oertli et al. 2002), flow, size, and permanence regimes (De Bie et al. 2010) as well as early and late successional stages (Hassall et al. 2012) of ponds on the landscape. Consequently, a fundamental aspect for biodiversity preservation of these ecosystems is that by ensuring the

diversity of waterbody types, aquatic biodiversity would be maximized. This would constitute an important aspect of biodiversity conservation plans.

Natural ecosystems within urban environments constitute attractive sites from which people can benefit. Indeed, they can be considered a peaceful getaway from the city life and a place to relax and reconnect with nature. In general, public perception of wetlands in their vicinity is positive and they are usually considered an asset (Kaplowitz and Kerr 2003, Manuel 2003, Johnson and Pflugh 2008). However, the benefits that people obtain from urban ecosystems and the relationship between site attractiveness and biodiversity is not completely known, and not necessarily direct. Biodiversity can be perceived and related to psychological well-being, but these differ between taxonomic groups, as well as people's perception of diversity. Consequently, meeting both public well-being and biodiversity can be a difficult operation, as the relationship is surely multiple and very complex (Fuller et al. 2007, Dallimer et al. 2012). Furthermore, citizens mostly enjoy and preserve taxa that are visually attractive, or appeal to their emotions. Consequently, taxa that are less conspicuous, appealing or known to the general public can be excluded from conservation plans. This may especially be true for taxa such as zooplankton, which even though they are less conspicuous and known to the general public, remain important ecological actors and constitute an essential component of freshwater ecosystems.

Zooplankton are important actors in aquatic food webs, as they play a central role in aquatic food webs, regulating the flow of nutrients from algae and bacteria to higher trophic levels (McQueen et al. 1986, Finlay et al. 2007, Gélinas et al. 2007). Knowledge of zooplankton species distribution patterns, and of their ecology may also have practical uses such as the control of undesirable phytoplankton biomass, leading to cleaner and clearer

waters (Peretyatko et al. 2009, Teissier et al. 2011), or as biological tools to assess water quality or contamination by waterborne parasites (Gannon and Stemberger 1978, Walseng et al. 2003, Nowosad et al. 2007). Furthermore, zooplankton have also been strongly advocated as biological indicators of ecological quality (Jeppesen et al. 2011). Consequently, the study of their ecology and biodiversity patterns should be an important part of aquatic ecosystem studies. However, while zooplankton communities in deeper, larger lakes are well studied, the ecology of zooplankton communities in urban environments remains largely unknown.

From the few studies that have focused on various components of urban zooplankton communities, different aspects of their ecology can be understood. Their communities and diversity are related to environmental characteristics such as land use, water chemistry and aquatic vegetation (Dodson et al. 2005, Dodson 2008), but they can be affected and modified by human activities (Langley et al. 1995, Moore et al. 2000, Van Meter and Swan 2014). However, despite exposure to anthropogenic stressors and human activities, urban waterbodies can contain noticeable amounts of zooplankton biodiversity and are not necessarily less diverse than their more natural or undamaged counterparts (Langley et al. 1995, Ejsmont-Karabin and Kuczyńska-Kippen 2001) and thus they may represent important reservoirs for zooplankton biodiversity. Finally, strong seasonal variation can be observed (Burdíková et al. 2012). These studies show urban zooplankton communities as diverse and dynamic assemblages that vary in response to various factors, both natural and anthropogenic.

More studies are needed to establish a reference point for zooplankton communities in urban waterbodies, as well as allow a better definition of their biodiversity and their sources of variation. Indeed, even though several studies have been conducted on urban pond communities, some groups, such as amphibians, have received more attention than others

(Hassall 2014). Given the importance of zooplankton communities in natural aquatic environments, increased knowledge of their ecology in urban environments will provide a better idea of urban pond functioning, help understand the effects of anthropogenic stressors on aquatic communities, as well as determine the biodiversity potential of urban ponds.

1.5 Study sites

The city of Montreal (45.46 - 45.69ºN, 73.50 - 73.90ºW) is located in the Canadian province of Quebec. The city is an island located at the junction of the Saint Lawrence and Ottawa rivers. With a surface area of approximately 499.19 km^2, it is not amongst the largest freshwater islands in the world. However, it is the most densely populated freshwater island in the world, with a population of 1 886 481 people in 2011 (Statistics Canada 2012). Furthermore, it is the second most populous city in Canada and amongst the ten most populous cities of North America. Several waterbodies are present on the island, some artificially created, and serving a variety of socio-economic functions. Many of these waterbodies are used for leisure or recreational activities, and are often visited by people. During the summers of 2010 and 2011, a group of 20 waterbodies of various types were sampled to evaluate zooplankton biodiversity in these aquatic habitats. The waterbodies were sampled in July of 2010 and in June, July and August of 2011. These waterbodies were quite distant from each other and were not connected to each other, which imply that they should not form a metacommunity. All studied waterbodies were located within the urban agglomeration of Montreal. Thus, they fall under the same jurisdiction, being subject to the same potential management practices and are visited by the same human population.

While interest in pond biodiversity has seen an increase over the last years (Oertli et al. 2009), there is a lot of uncertainty around the term "pond" itself, as it refers to a wide array of small waterbody types (Biggs et al. 2005, De Meester et al. 2005, Oertli et al. 2005a, Boix et al. 2012). The majority of our studied waterbodies fall into this broad category, although the larger ones could also be considered small lakes and thus, all will usually be referred to as "waterbodies". Furthermore, given that one of the interests of our study was in assessing and determining the biodiversity present in aquatic habitats within an urban environment, we wanted to include the full variety of urban aquatic habitats to which zooplankton communities are exposed.

The sampled waterbodies covered a wide range of types and included both permanent and temporary waterbodies, as well as three wetlands. Based on observations in 2010 and a visual campaign that focused on the vegetation cover and dominance in 2012, fourteen waterbodies had aquatic vegetation in the littoral zone composed mainly of emergent (*Phragmites*, *Typha*, *Scirpus*, *Lythrum*, *Equisetum*, *Sparganium*, *Pontederia*, *Butomus*, *Alisma*), floating (*Nymphaea*, *Nymphoïdes, Lemna*, *Wolffia*) or submerged (*Potamogeton*, *Ceratophyllum, Anacharis* (*Elodea*), *Utricularia*, *Myriophyllum*, *Valisneria*, *Najas*) plants and some Characeae algae (*Nitella flexilis*, *Chara vulgaris*). They also showed a variety of substrate types, with some of these waterbodies being lined with soil, mud, gravel and sometimes bare concrete. On average, waterbody size (surface and mean depth) were variable. However, except for a single waterbody, most were shallow, usually no deeper than 1.91 m. Fish communities were noted as being present in all but three waterbodies.

1.6 Structure and objectives of this thesis

The main interest of this study was to evaluate the biodiversity potential and understand biodiversity patterns of zooplankton communities of waterbodies located in an urban setting. Further interests include the determination of the most important sources of zooplankton biodiversity variation, an assessment of the conservation value of waterbodies, as well as suggestions for biodiversity preservation. This doctoral thesis is organized into five chapters. The first chapter introduces the general setting and places the study in the current ecological context. The following three chapters are presented as research articles, each with a different research objective. The fifth chapter concludes on the study and underlines what it has brought to the advancement of knowledge regarding small waterbody ecology, while also suggesting possible openings and perspectives.

The first research objective was to examine biodiversity patterns of zooplankton communities across eighteen waterbodies in the urban landscape of Montreal to determine the main sources of variation in urban zooplankton communities. Indeed, given the possible importance of aquatic biodiversity in urban ponds, a solid understanding of aquatic species distributions in urban aquatic habitats will be necessary to advance urban ecology and preserve biodiversity in cities. We tested the hypothesis that, within zooplankton taxonomic groups (rotifers, cladocerans and copepods), asexual and fast-growing species such as rotifers and cladocerans would contribute more to biodiversity than sexual and slow-growing species such as copepods. We also expected to see variability in zooplankton communities within waterbodies, with the littoral vegetated zones of waterbodies, offering structurally more complex habitat and a refuge from some predators, being important habitats for zooplankton biodiversity and contributing considerably to the species richness pool. Finally, as for non-

urban lakes, we expected communities to respond to multiple abiotic and biotic environmental conditions, but that management practices would also play an important role. To verify these claims, a multi-scale sampling design at regional (among waterbodies) and local (littoral and pelagic zones within each waterbody) scales was applied. These questions do not only help evaluate the biodiversity potential of urban waterbodies, but will also be important in guiding future management practices to best favour urban biodiversity and water quality.

The second research objective was to explore the phylogenetic diversity of cladocerans communities in urban waterbodies on the Island of Montreal and suggest conservation plans to best preserve phylogenetic diversity of aquatic communities. We also evaluated the consequences of phylogenetic uncertainty on phylogenetic conservation and how it would affect the prioritization of sites. To verify this, we sampled nineteen waterbodies in the months of June, July and August of 2011 in order to determine cladoceran species assemblages. Based on DNA sequences from two mitochondrial genes, phylogenetic trees for the sampled species and several other cladocerans taxa were inferred using Bayesian inference. Using the posterior distribution of trees, we considered the extent to which uncertainty in the phylogenetic tree affected the results and how comparison of phylogenetic diversity between sites could be carried out. We found that waterbodies on the Island of Montreal showed variability with regards to phylogenetic diversity and that careful selection of which sites to prioritize could lead to preserving a maximal amount of phylogenetic diversity. However, when phylogenetic uncertainty was taken into account, several potential comparisons between sites were not given any support. Consequently, in the presence of phylogenetic uncertainty, prioritization ranks become unresolved and prioritization should thus be determined more cautiously. Variability in the phylogenetic estimates should be consistently considered and integrated into

estimates of phylogenetic diversity and conservation decisions to avoid making suboptimal choices.

The third and last research objective was to describe and understand monthly variation in community composition and feeding group patterns, as well as explain richness and diversity patterns of zooplankton communities in a set of 19 urban waterbodies that were followed monthly, from June to August of 2011. The small size and relatively high rates of population increase means that zooplankton comprises a dynamic ecological component that can change over time. Considering the fact that species composition can change over time, we tested the hypothesis that this relationship between waterbodies and their littoral zones changes over time. By characterizing communities using information on species feeding ecology, we also tested the hypothesis that urbanization and anthropic stressors in urban waterbodies would lead to a single feeding group pattern. Finally, knowledge of the main drivers of zooplankton species richness and community composition will be crucial in allowing the elaboration of biodiversity conservation plans. To this end, we used a set of five environmental variables (total phosphorus concentration, surface area, mean depth, mean Secchi depth and macrophyte cover), which have been noted as being important for aquatic biodiversity in order to see how they affected zooplankton species richness in our urban waterbodies.

Chapter 2

Assessing aquatic biodiversity of zooplankton communities in an urban landscape

Authors: El-Amine Mimouni, Bernadette Pinel-Alloul and Beatrix E. Beisner

2.1 Abstract

Aquatic ecosystems are common in urban environments. A solid understanding of aquatic species distributions in urban habitats will both advance urban ecology and preserve biodiversity in cities. In particular, zooplankton are central components of aquatic food webs and their biodiversity patterns thus warrant further characterization and understanding. We examined sources of variation and biodiversity patterns of zooplankton communities across eighteen waterbodies in the urban landscape of Canada's large island city of Montreal. We report a total of 80 zooplankton taxa of which rotifers and cladocerans were major contributing taxa to biodiversity. We found a lack of agreement between contributions of individual waterbodies to rotifer and cladoceran beta diversity. Littoral vegetated zones proved to be important habitats for zooplankton biodiversity, contributing considerably to the species richness pool, often with a different species composition. Further variation in zooplankton community composition was attributable to local factors such as waterbody size, algal biomass and composition, and macroinvertebrate predators, but also to urban management practices such as waterbody draining during winter. We show that urban waterbodies can represent important reservoirs of biodiversity. Management practices favouring a large diversity of permanent and temporary habitats with littoral vegetated zones should be incorporated in urban design and conservation plans.

Keywords: Biodiversity, zooplankton, community structure, urban ecology, littoral zone

2.2 Introduction

Freshwater ecologists have traditionally focused on large waterbodies, such as lakes, streams and rivers. In contrast, shallow lakes and ponds, occurring far more frequently than larger lakes (Downing et al. 2006, Downing 2010) and often in urban environments, are less studied. Recently, a high potential for endemicity and species richness, especially in urban ponds and man-made waterbodies has been revealed, with important consequences for landscape biodiversity (Langley et al. 1995, Maier et al. 1998, Ejsmont-Karabin and Kuczyńska-Kippen 2001, De Bie et al. 2010). Indeed, the amount of environmental heterogeneity across urban landscapes, coupled with the large number of waterbodies in many cities should allow for the creation of a complex mosaic of ecosystems within which biodiversity is promoted at local and regional scales. The high overall contribution of small urban waterbodies to diversity, in line with the SLoSS ("Single Large or Several Small") debate, would call for their study and inventorying to enable their conservation (Oertli et al. 2002). Furthermore, ponds also represent key ecosystems that are especially amenable to the testing of ecological and evolutionary hypotheses (De Meester et al. 2005, De Bie et al. 2012). As such, a number of programs have been developed to assess and monitor their ecological status and biodiversity in Europe (Moss et al. 2003, Oertli et al. 2005, Declerck et al. 2006, Céréghino et al. 2008). However, relative to the knowledge gained on small man-made lakes and urban ponds in Europe, knowledge about aquatic biodiversity in urban environments is scant in North America, where cities are, by nature, structurally different.

In the field of "urban ecology" a better understanding of biodiversity patterns, as well as the structure and function of populations, communities and ecosystems in urban landscapes are sought (Pickett et al. 1997, Collins et al. 2000, McDonnell and Hahs 2013). Aquatic

communities in urban environments may be exposed to suites of factors that are considerably different from those occurring in more natural environments. Thus, their biodiversity merits investigation for this reason. Furthermore, owing to their proximity to city centers and human stressors, studying urban waterbodies may be the most direct approach for assessing the effects of anthropogenic stressors on biodiversity and communities, as well as developing management policies favouring biodiversity conservation.

The use of zooplankton communities, both as indicators of water quality and biodiversity in aquatic systems, is appealing because these communities tend to respond quickly to changes in their environment such as watershed land-use, water chemistry and trophic status (Pinel-Alloul et al. 1990, Patoine et al. 2002, Dodson et al. 2005). Additionally, in temporary ponds, habitat permanence and hydroperiod length can also affect both zooplankton species richness and community composition (Serrano and Fahd 2005, Boven and Brendonck 2009, Drenner et al. 2009). Zooplankton communities respond to food web changes in algal resources as well as to predation by fish and invertebrates, which makes them key actors in aquatic food webs, playing a fundamental role in the flow of nutrients from algae and bacteria to higher trophic levels (McQueen et al. 1986, Finlay et al. 2007, Gélinas et al. 2007).

These intimate relationships with both their biotic and abiotic environments have enabled the use of zooplankton as bioindicators of water quality (Gannon and Stemberger 1978, Pinel-Alloul et al. 1990, Moss et al. 2003, Boix et al. 2005, Nowosad et al. 2007). Moreover, through their efficient grazing, large cladocerans can help maintain clear waters that are aesthetically desired in ponds, and their preservation should aid in restoration management practices (Peretyatko et al. 2009 and 2012). Additionally, zooplankton may also

play a role in human health, being able to reduce protozoan pathogen activity through grazing (Fayer et al. 2000, Connelly et al. 2007), but also by affecting pathogen growth and incidence (Tamplin et al. 1990, De Magny et al. 2011). As such, increased knowledge of zooplankton communities and the factors structuring these biota in urban ecosystems can be of direct benefit to humans by enabling and guiding more natural and safer management practices for aquatic environments.

In this study, we used zooplankton, central players in aquatic food webs, to identify and describe patterns of variation in diversity across a variety of waterbodies in Montreal (QC), a large Canadian city. With respect to urban biodiversity patterns, we asked (i) which zooplankton taxonomic groups (rotifers, cladocerans and copepods) and (ii) which habitats (waterbodies) and zones (littoral vs. pelagic) contributed the most to the aquatic diversity of the regional species pool (gamma diversity) as well as to beta diversity? As rotifers and cladocerans reproduce mainly by asexual reproduction (parthenogenesis) and have short generation times, while copepods reproduce through obligatory sexual reproduction and have long generation times, we expected that rotifers and cladocerans would have larger populations and dominate zooplankton communities, therefore contributing more than copepods to gamma and beta diversity. Given that littoral zones favour zooplankton biodiversity in more natural north temperate lakes (Walseng et al. 2006), we predicted that urban waterbodies containing a vegetated littoral zone would contribute more to gamma diversity, and that more complex littoral zones would support more species and a different community composition than the pelagic zone. Finally, we asked (iii) which factors, amongst a suite of measured environmental variables, including land-use and management techniques, most affected zooplankton community composition patterns in urban waterbodies? As for non-

urban lakes, we expected communities to respond to multiple abiotic and biotic environmental conditions (Pinel-Alloul et al. 1995), but that management practices would also play an important role. These questions do not only help evaluate the biodiversity potential of urban waterbodies, but will also be important in guiding future management practices to best favour urban biodiversity and water quality.

2.3 Methods

2.3.1 Study sites and sampling design

Between the 7th and the 23rd of July 2010, 18 waterbodies of various types (including both permanent and temporary waterbodies, as well as three wetlands), distributed over the Island of Montreal (Quebec, Canada) (45.46 - 45.69ºN, 73.50 - 73.90ºW), were sampled to evaluate zooplankton biodiversity in urban environments (Figure 2.1). These waterbodies were selected to represent the various freshwater ecosystems observed on the Island of Montreal and are surveyed by the city water-quality monitoring program (Réseau de Suivi du Milieu Aquatique: http://ville.montreal.qc.ca), providing us with data about management practices in each waterbody and human residential density in the surrounding landscape.
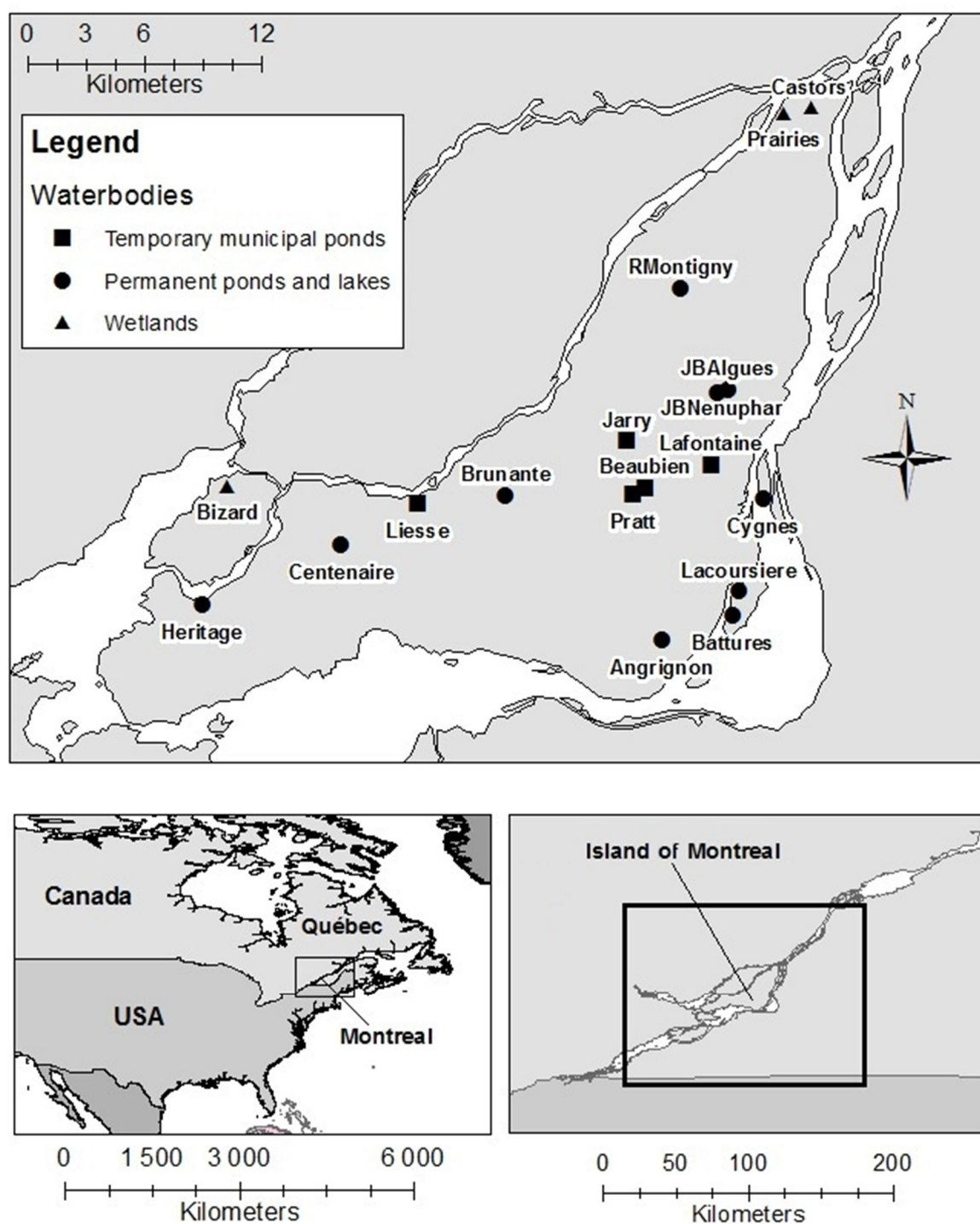
Figure 2.1: Geographic location and distribution of the 18 sampled waterbodies during the summer of 2010 on the Island of Montreal (Quebec, Canada). Modified from Pinel-Alloul and Mimouni, 2013.

To permit multiple comparisons of zooplankton community composition patterns both among and within waterbodies, we applied a multi-scale sampling design at regional (among waterbodies) and local (littoral and pelagic zones within each waterbody) scales. The littoral and pelagic zones of each waterbody were sampled separately by randomly choosing three sampling points in the littoral zone, along with three pelagic points in the open-water area directly in front of these, resulting in a total of six sampling points per waterbody. Zooplankton was sampled at each sampling location from a small anchored boat using a 3 L bucket that was dipped ten times to arm's length in surface water. The 30 L total water sampling unit was subsequently filtered through a 54 μm mesh size plankton net. Organisms were first narcotized with carbonated water and fixed with pure formaldehyde.

Maximum depth and water transparency were measured using a Secchi disk at the three pelagic sampling points, with the results averaged to obtain a single waterbody estimate. Phytoplankton biomass, estimated as total chlorophyll *a*, as well as biomass for four spectral groups of algae (Greens: chlorophytes, Cyanos: cyanophytes containing phycocyanin, Browns: diatoms + chrysophytes + dinoflagellates, Cryptos: cryptophytes + cyanophytes containing phycoerythrin) was also determined at these same pelagic sampling points using a bbe FluoroProbe (Beutler et al. 2002, Longhi and Beisner 2009).

To assess the abundance of potential invertebrate predators, these were sampled at the same sampling points as zooplankton. Littoral macroinvertebrates were sampled with a rectangular kick net (46x23 cm opening, 500-μm mesh size) that was pushed up to 2 cm into the substrate and dragged over 1.5 m of sediment surface. Pelagic macroinvertebrates were sampled using a 4 L Ekman grab sampler. Macroinvertebrate sampling units were sifted through 500 μm and 1 mm mesh sieves on sampling sites. Both size-fractions were combined

and preserved in 75% ethanol solution and stained with Rose Bengal solution. The presence or absence of fish in each waterbody was confirmed by city managers, visual observations and occasional captures during sampling.

2.3.2 Taxonomic analyses

In the laboratory, zooplankton sampling units were kept in formaldehyde for one month to fix the organisms and then transferred to a 75% ethanol and 5% glycerol solution to avoid desiccation, being concentrated into 25 mL scintillation vials and stained using Rose Bengal solution. Except for when densities were too high, a quarter of each well-mixed zooplankton sampling unit was taken using a pipette with a large-mouthed tip and transferred to a Ward counting wheel (Ward 1955). Taxa were enumerated under a Leica Wild M3B stereomicroscope and identified with a Wild Heerbrug microscope to the finest possible taxonomic resolution (species and genus) using taxonomic keys for Rotifera (Edmondson 1959, Stemberger 1979, Nogrady et al. 1995, Haney et al. 2010), Cladocera (Brooks 1959, Hebert 1995, Haney et al. 2010) and Copepoda (Smith and Fernando 1978, Hudson and Lesko 2003).

Macroinvertebrate sampling units were again separated onto a 500-μm mesh sieve to eliminate small detritus and organic matter in the laboratory. Macroinvertebrates were sorted and counted under a dissecting microscope, being identified to family level using Merritt and Cummins (1996) and Smith (2001). For each sampling unit, total abundances of insect larvae known to be potential predators of zooplankton (Chaoboridae, Corixidae, Notonectidae, Gerridae, Veliidae, Pleidae, Haliplidae, Dytiscidae, Coenogradidae, Aeshnidae, Libellulinae) were estimated.

2.3.3 Data analyses

Diversity analyses – Gamma diversity was estimated as the cumulative species richness (Gaston and Spicer 2004) of all sampled waterbodies in the urban area and partitioned to estimate the contribution of sites and zooplankton taxonomic groups (Cladocera, Copepoda, Rotifera). Total beta diversity was expressed as the variance of the Hellinger-transformed community data table across all sampling units (Legendre et al. 2005). Total beta diversity was partitioned into species contributions (SCBD: degree of variation of individual taxa across the study area) and local contributions (LCBD: comparative indicators of the ecological uniqueness of the sampling units) by calculating the marginal sums of squares of the transformed zooplankton community data-table (Legendre and De Cáceres 2013). In our case, the sums of squares were computed for all 108 sampling units and all recorded taxa, and these values were summed according to waterbody identity and zooplankton taxonomic groups (cladocerans, copepods and rotifers).

Univariate and multivariate analyses of variance – To evaluate the differences in zooplankton beta diversity and community composition in waterbodies with a vegetated littoral zone, we considered a suite of biodiversity metrics. These metrics included the Euclidean distance between species richness of sampling units, the Jaccard dissimilarity (Jaccard 1908) in taxonomic composition between sampling units and the Hellinger distance (Rao 1995) in taxonomic densities between sampling units. These three metrics represent a continuum that gives increasing weight to community composition differences, ranging from a simple number (species richness), to a metric that takes into account species presence/absence data (Jaccard dissimilarity) and finally to a metric that incorporates the species relative abundances (Hellinger distance). Tests for differences between communities were carried out

using ANOVA (in the univariate case for species richness) and MANOVA (in the multivariate cases for the Jaccard and Hellinger metrics). Tests for homoscedasticity and homogeneity of the variance-covariance matrices were done using Levene's test (univariate case) and the method outlined in Anderson (2006) (multivariate case). In all three cases, these tests were not significant (p-value > 0.05). To account for the pairing in our sampling units, we performed paired comparison tests using the method described by Legendre in an unpublished appendix to the paper by Escobar-Briones et al. (2008). To adequately test for differences between zones, only sites with a littoral zone presenting either submerged or emergent rooted macrophytes were considered. The factors "Site" and "Zone" were crossed and replicated sampling allowed for the testing of an interaction between them. These factors were coded as orthogonal Helmert contrasts and used in order to carry out two-way MANOVA. In all cases, the algorithm of McArdle and Anderson (2001), which computes the F-statistic by using the Gower-centered distance matrix, was used, alleviating the need for any correction for negative eigenvalues. Tests of the interaction were done by using the Helmert variables coding for the interaction as explanatory variables, with the Helmert variables coding for both studied factors ("Site" and "Zone"), as well as the principal components for the 28 axes that did not have null eigenvalues of the regression of dummy variables representing the pairs of sampling units onto the factor "Site".

Interpreting interactions - We interpreted the interaction between the factors "Site" and "Zone" in the univariate case for species richness using an interaction plot. To further explore the multivariate interactions, interaction maps (Legendre et al. 2010) were created, by attributing numbers to the sampling units according to their groups as determined by a k-means clustering and the optimal number of clusters to consider determined by the Caliński-

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Harabasz criterion (1974). For the Jaccard dissimilarity, a principal coordinate analysis (Gower 1966) was carried out using the square root of this dissimilarity, which is a Euclidean metric and will therefore produce no negative eigenvalues (Gower and Legendre 1986). All obtained axes were retained and used in the k-means analysis. For the Hellinger distance, the maximum was found at k = 11, but for the Jaccard dissimilarity, the criterion showed no clear maximum beyond k = 2. In this case, we also considered the SSI criterion (Borcard et al. 2011), which showed a maximum at k = 20.

Redundancy analysis - To identify how the different sets of environmental variables, *i)* management practices, *ii)* pond morphology, water quality, trophic state and *iii)* fish and predatory macroinvertebrates affected zooplankton communities, a redundancy analysis (RDA) was carried out using all three sets of environmental variables together as explanatory variables and the Hellinger-transformed species-composition data as response variables. Certain explanatory variables had a single averaged value repeated for all sampling units within a site. For example, the mean biomass of chlorophyll *a* and that of the various spectral groups of algae provided a general idea of the biomass of algae and trophic state in waterbodies. Other variables, such as management practices (whether the waterbody is drained during winter), for which only a single value for each waterbody existed, similarly related to the entire waterbody. Prior to the analysis, environmental variables were individually transformed to reduce skewness (Legendre and Legendre 2012). Macrophyte cover (in %) was not transformed, Greens and Browns algal concentrations as well as total chlorophyll *a* concentration ($\mu g.L^{-1}$), maximum depth and Secchi depth (m) were $\log_e$ transformed; Cyanos and Cryptos algal concentrations ($\mu g.L^{-1}$) and surface area (m^2) were 4th root transformed and

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all macroinvertebrate abundances were $\log_e(x+1)$ transformed. Contrary to the analyses of variance, the redundancy analysis considered all 18 waterbodies.

All statistical analyses were carried out in R 2.15.2 (R Development Core Team 2012) along with various functions from the packages *MASS* (Venables and Ripley 2002), *ape* (Paradis et al. 2004), *ade4* (Dray and Dufour 2007), *rdaTest* (Legendre and Durand 2010) and *vegan* (Oksanen et al. 2012).

2.4 Results

2.4.1 Site environmental features

Waterbodies were evenly distributed in areas of low, medium and high urban residential density (six per class), based on city classification (Table 2.1). Five waterbodies were temporary, being drained in winter and refilled each year. Based on observations in 2010 and a visual campaign of the vegetation cover and dominance in 2012, fourteen waterbodies had aquatic vegetation in the littoral zone composed mainly of emergent (*Phragmites*, *Typha*, *Scirpus*, *Lythrum*, *Equisetum*, *Sparganium*, *Pontederia*, *Butomus*, *Alisma*), floating (*Nymphaea*, *Nymphoïdes, Lemna*, *Wolffia*) or submerged (*Potamogeton*, *Ceratophyllum, Anacharis* (*Elodea*), *Utricularia*, *Myriophyllum*, *Valisneria*, *Najas*) plants and some Characeae algae (*Nitella flexilis*, *Chara vulgaris*). On average, waterbody size (surface and mean depth) and Secchi depth were quite variable and, in some shallow ponds, light reached the sediments even in the open water zone. Fish communities were present in all but three waterbodies. Macroinvertebrate abundances were highly variable among families and

sampling sites, with the most abundant groups belonging to Hemiptera (Pleidae, Notonectidae, Corixidae, and Vellidae) and Odonata (Coenagrionidae).

Table 2.1: General characteristics of the landscape and management practices, water quality, trophic conditions, fish and macroinvertebrates variables of the 18 studied urban waterbodies.

Residential land use and management practices			
Winter draining		Yes (5)	No (13)
Macrophytes		Yes (14)	No (4)
Urban density	Low (6)	Medium (6)	High (6)

Morphometry, water quality and trophic state			
	Mean	Standard deviation	Minimum	Maximum
Mean depth (m)	2.01	2.41	0.30	11.00
Secchi (m)	1.05	0.82	0.30	3.73
Surface (m^2)	28 007.76	35 313.40	392.12	114 466.65
Chl.a (µg.L^{-1})	13.30	16.40	1.10	64.06
Browns (µg.L^{-1})	2.98	4.56	0.02	14.41
Cryptos (µg.L^{-1})	1.30	4.17	0.00	17.89
Cyanos (µg.L^{-1})	1.49	2.58	0.00	9.77
Greens (µg.L^{-1})	7.53	11.23	0.38	44.13
Macrophyte cover (%)	44.72	35.91	0.00	100.00

Fish and macroinvertebrate predators			
Fish		Presence (15)	Absence (3)
	Mean	Standard deviation	Minimum	Maximum
Aeshnidae (ind.sampling unit^{-1})	1.01	2.18	0.00	8.17
Libellulidae (ind.samping unit^{-1})	1.23	1.77	0.00	5.67
Coenagrionidae (ind.sampling unit^{-1})	13.30	30.53	0.00	130.33
Corixidae (ind.sampling unit^{-1})	7.88	10.25	0.00	30.67
Notonectidae (ind.sampling unit^{-1})	9.30	26.51	0.00	108.50
Pleidae (ind.sampling unit^{-1})	14.39	53.98	0.00	230.33
Gerridae (ind.sampling unit^{-1})	0.81	1.75	0.00	7.33
Veliidae (ind.sampling unit^{-1})	9.15	21.65	0.00	72.00
Dytiscidae (ind.sampling unit^{-1})	1.00	1.40	0.00	3.67
Haliplidae (ind.sampling unit^{-1})	3.31	6.04	0.00	24.00
Chaoboridae (ind.sampling unit^{-1})	0.79	2.73	0.00	11.67

2.4.2 Zooplankton species richness and taxonomic assemblages

Gamma diversity recorded across all 18 waterbodies in the urban region accounted for a total of 80 zooplankton taxa. The full taxonomic list of taxa is presented in Appendix 1. Rotifers were the most diverse, being represented by 45 taxa. Most of the 35 crustacean taxa were cladocerans (26 taxa). Copepods were the least diverse group, being represented by nine taxa, of which six were cyclopoids and three were calanoids. Zooplankton total species richness varied from 6 to 35 taxa among waterbodies (1 to 24 for rotifers, 2 to 14 for cladocerans and 0 to 5 for copepods) (Table 2.2A). Most waterbodies had a more or less equal proportion of cladoceran and rotifer species, but communities showed a gradient from being dominated by cladocerans to rotifers (Figure 2.2). Species richness per sampling unit varied from 2 to 26 taxa, with a mean value of 10 taxa. All zooplankton groups had sampling units for which no taxa were recorded, but differed in their range of recorded taxa, with rotifers (0 to 18) and cladocerans (0 to 13) having higher upper values than copepods (0 to 4).

Table 2.2: Contributions of the zooplankton community and taxonomic assemblages of each studied waterbody to species richness (A) and beta diversity (B) in the urban region. Values for beta diversity correspond to the contributions of studied sites (LCBD) and zooplankton assemblages (SCDB) to beta diversity; they were divided by the total sums-of-squares and multiplied by 100 to obtain percentages.

Waterbody name	A - Species richness				B - Beta diversity			
	Cladocerans	Copepods	Rotifers	Total	Cladocerans	Copepods	Rotifers	Total
Beaubien	6	1	1	8	6.36	0.02	1.02	7.41
Liesse	6	0	3	9	6.11	0.02	1.25	7.38
Lafontaine	7	0	5	12	5.23	0.02	1.27	6.52
Jarry	10	0	10	20	4.04	0.02	0.96	5.02
Cygnes	11	2	9	22	3.66	0.38	1.89	5.93
Battures	10	5	14	29	3.02	0.09	1.71	4.82
JBNenuphars	12	4	13	29	1.61	0.87	2.01	4.49
Centenaire	2	1	3	6	1.66	0.1	2.27	4.03
Angrignon	14	3	10	27	1.29	0.04	2.59	3.92
Heritage	7	0	12	19	0.96	0.02	3.28	4.26
JBAlgues	8	3	14	25	0.77	0.36	3.53	4.67
Brunante	10	4	16	30	1.25	0.14	4.36	5.76
Pratt	3	1	4	8	1.63	0.02	4.87	6.53
Castors	6	4	15	25	0.66	0.88	3.93	5.46
Prairies	3	3	16	22	0.71	0.05	4.24	5.01
Bizard	8	3	24	35	0.68	0.03	5.10	5.81
Lacoursiere	4	3	6	13	0.57	0.83	5.06	6.46
RMontigny	7	3	9	19	0.69	0.04	5.79	6.52
Total	26	9	45	80	40.91	3.94	55.16	100
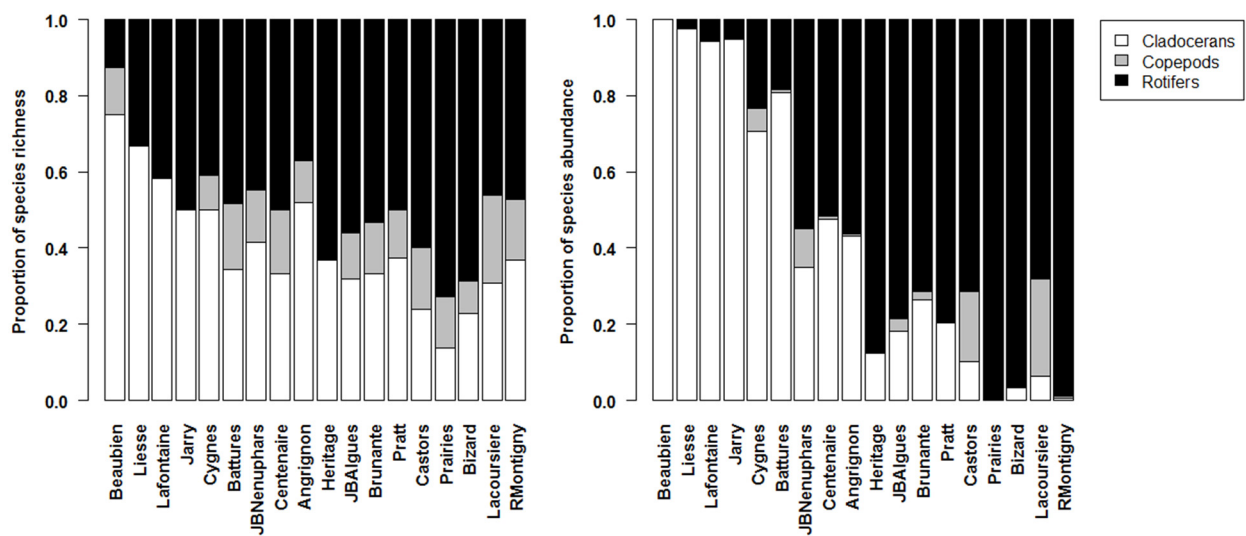
Figure 2.2: Barplots showing the proportional species richness (left) and species abundance (right) between the zooplankton assemblages (Cladocerans, Copepods and Rotifers) for the 18 waterbodies.

No taxa were ubiquitous across all 18 waterbodies, although some taxa showed high incidences: *Alona* spp. was found in 15 sites, *Polyarthra* spp. in 14, *Bosminidae* spp. and *Chydorus* spp. in 13, *Diaphanosoma* sp., *Keratella* sp. and *Lecane* (*Monostyla*) spp. in 12, *Scapholeberis* sp. in 11, and *Eucyclops* cf. *pectinifer*, *Dissotrocha* sp., *Mytilina* cf. *ventralis* and *Platyias quadricornis* in 10 (see Appendix 1). On the other hand, approximately one third (28) of the taxa were recorded in only a single waterbody. Such rarity was also evident from the fact that out of those 28 taxa, 11 were found in only a single replicate out of the six sampling units collected in each waterbody (data not shown).

2.4.3 Contribution of sites, zooplankton groups and taxa to beta diversity

When expressed as percentages of total beta diversity, contributions of sites (LCBD) varied from a minimum of 3.92% to a maximum of 7.41% (Table 2.2B). The waterbodies Beaubien, Liesse, Lafontaine, Cygnes and Lacoursiere contained sampling units that had significant LCBD values. However, when these waterbody LCBD values for the entire zooplankton community were summed up according to zooplankton groups (Cladocera, Copepoda, Rotifera), more pronounced differences arose. Indeed, some waterbodies (Beaubien, Liesse and Lafontaine) contributed more to cladoceran beta diversity whereas others (RMontigny, Bizard and Lacoursiere) contributed more to rotifer beta diversity. There was a strong negative relationship between waterbodies' cladoceran and rotifer LCBD values ($r = -0.81$; Figure 2.3).
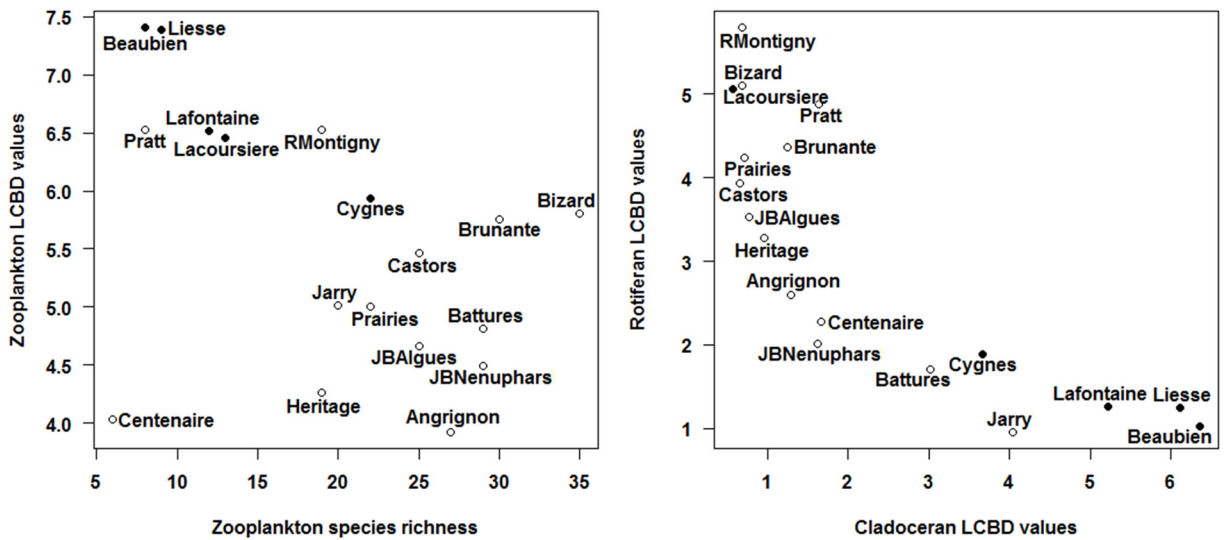
Figure 2.3: Scatterplots showing the relationship between zooplankton species richness and zooplankton LCBD values (left) and cladoceran and rotifer LCBD values (right) for the 18 waterbodies. The names of the waterbodies are indicated next to each point. Waterbodies which had sampling units with significant LCBD valyes are represented by a filled circle.

Excluding Centenaire, a large waterbody with some unique features (high densities of young-of-year fish, large duck populations whose faeces can significantly affect water quality, garbage dumping; together, these conditions may have produced low species richness and beta diversity), we observed a negative relationship between waterbody species richness and contribution to zooplankton beta diversity (r = -0.68; Figure 2.3). This may imply that the high contribution by some waterbodies to beta diversity was mostly the result of a few species that were rarely found elsewhere or did not make up important proportions of community composition. On one hand, sites such as Beaubien, Liesse and Lafontaine showed low species richness, but had the highest contribution to cladoceran beta diversity because their communities were dominated by a few taxa (*Ceriodaphnia reticulata*, *Ceriodaphnia* sp., *Daphnia* spp.) that were mostly absent or had very low densities in other sites. Similarly, RMontigny, Lacoursiere and Pratt showed among the highest contributions to rotifer beta diversity because of the populations of a few taxa (*Keratella tecta*, *Platyias patulus*, *Polyarthra* spp., *Lecane* sp. and *Lecane* (*Monostyla*) spp.) that dominated their communities. On the other hand, waterbodies with high species richness such as Angrignon, Battures and JBNenuphars did not show high contributions to zooplankton beta diversity because they supported diverse communities with taxa that did not make up important proportions of community composition or that were found in other waterbodies.

Out of the three taxonomic groups, cladocerans and rotifers contributed together to almost all of beta diversity (96.06%), accounting respectively for 40.91 and 55.16% of the zooplankton SCDB values (Table 2.2B). Copepods contributed very little, with the sum of their SCBD values being only 3.94%. The SCBD values of the different taxa were quite variable (Figure 2.4). Out of the 80 recorded taxa, 20 had SCBD values higher than the

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average SCBD value (1.25%). These species were mostly rotifers and cladocerans with the highest SCBD values for: *Keratella* sp. (10.06%), *Lecane* sp. (9.78%), Bosminidae spp. (9.75%), *Ceriodaphnia reticulata* (7.18%), *Ceriodaphnia* sp. (5.89%) and *Polyarthra* spp. (5.31%). Only two copepod species had SCBD values higher than the average: *Eucyclops* cf. *pectinifer* (1.71%) and *Skistodiaptomus oregonensis* (1.45%).

Figure 2.4: Barplot of the SCBD values in percentages for each of the 81 zooplankton taxa recorded across the 18 waterbodies with values sorted in decreasing order. Taxa with SCBD values higher than the average SCBD (1.25%) are indicated in black and taxa with values lower than the average SCBD value are in white. For taxon codes, see Appendix 1.
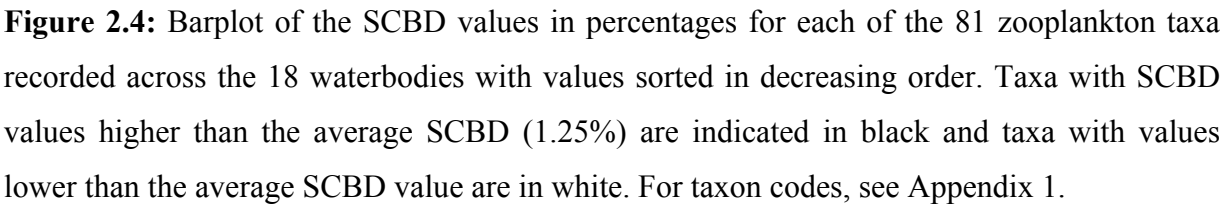
2.4.4 Analyses of variance and interactions

Significant interactions were found between the factors "Site" and "Zone" for all three biodiversity metrics (p-value < 0.05 after 9999 permutations). Owing to the significant interaction between Site and Zone for species richness in the univariate case, we compared mean species richness in the pelagic and littoral zones of each of the 14 sites that showed rooted macrophytes (Figure 2.5). Differences between zones, as shown by the slopes, were not consistent across sites and showed a large amount of variation. The slopes ranged from quasi-horizontal (e.g. Prairies, Liesse and Beaubien) to modest (e.g. Jarry to Bizard), indicating no or small differences in species richness of sampling units between the pelagic and littoral zones, to extremely steep (e.g. Battures to JBNenuphars), indicating noticeably higher species richness of sampling units in the littoral than in the pelagic zone.
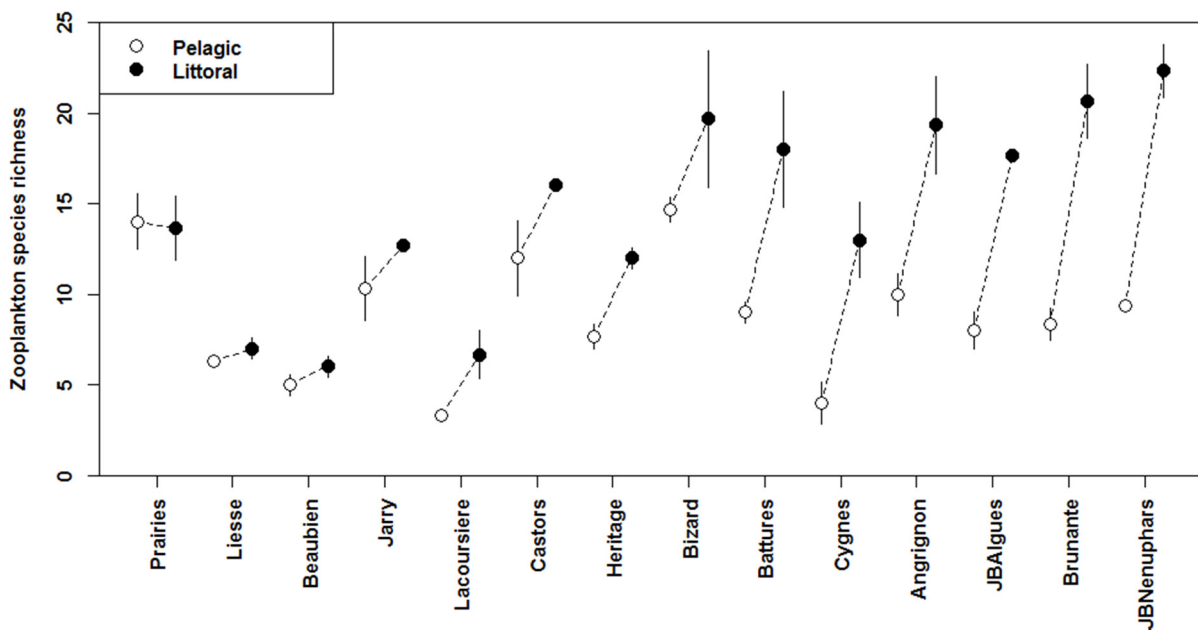
Figure 2.5: Average species richness (±1SE) within the pelagic and littoral zones for the 14 waterbodies with a well-developed littoral zone. Pelagic means are indicated with an open circle and littoral means with a full circle.

In the multivariate cases, the interaction maps showed that, when considering the Jaccard dissimilarity (Figure 2.6A), zooplankton communities in Beaubien, Bizard, Liesse, Jarry, Prairies and Castors differed from the other sites, as well as from each other, but their communities did not differ noticeably between the littoral and pelagic zones, with all of their sampling units being clustered within the same group. However, Brunante, Heritage, Lacoursiere, Battures, Cygnes, JBAlgues and JBNenuphars showed strong differences in community between the pelagic and littoral zones. The Hellinger distance also showed that some sites had different community compositions from the other sites (Beaubien, Brunante, Bizard, Liesse, Lacoursiere, Battures, Angrignon, Jarry and Prairies), and that these were undifferentiated between the two zones (Figure 2.6B). However, except for the waterbodies in the Botanical Garden (JBAlgues and JBNenuphars) and Heritage, the Hellinger distance did not show strong differences between the two zones. Stronger differences for the Jaccard dissimilarity than the Hellinger distance would imply that Angrignon, Battures and Cygnes may have different community assemblages in the littoral and pelagic zones, but similar dominant species.
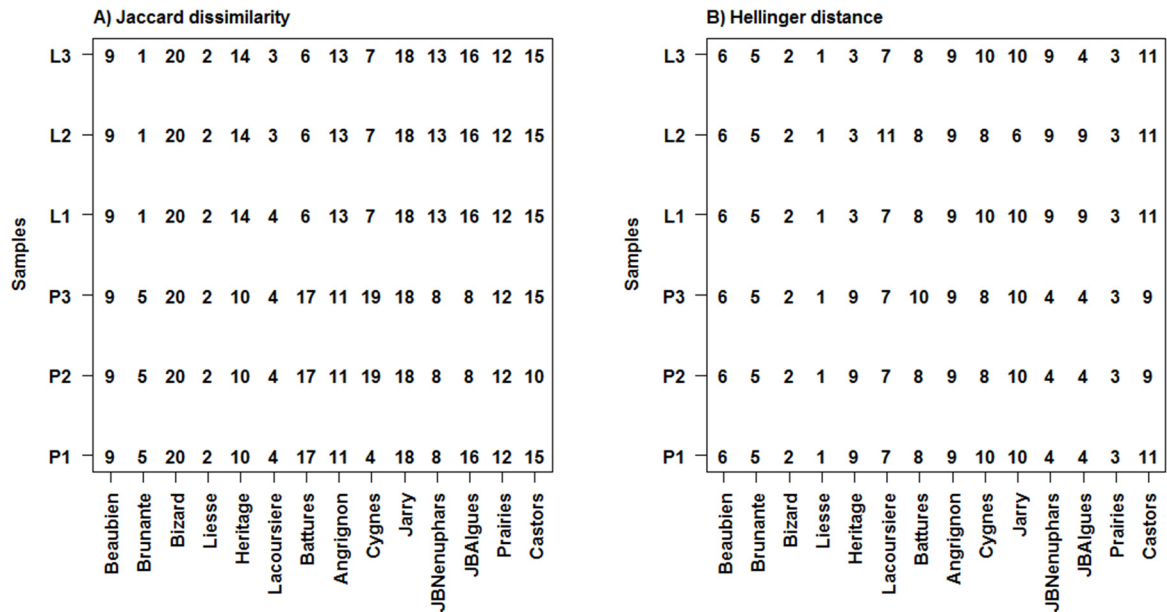
Figure 2.6: Interaction map showing the attribution of zooplankton sampling units to groups as determined by a k-means partitioning applied to the Jaccard dissimilarity principal coordinate axes (a, 20 groups) and the Hellinger-transformed zooplankton communities (b, 11 groups). Numbers for each sampling unit correspond to the partition to which it belongs. Site names are noted on the abscissa and sampling units (P1-P3 from pelagic zone and L1-L3 from littoral zone) on the ordinate. Numberings have meaning when compared within waterbodies as they represent paired sampling units, but not across waterbodies.

2.4.5 Redundancy analysis

The RDA model relating zooplankton community composition and the three sets of environmental variables was significant (p-value < 0.05 after 9999 permutations) and showed relationships between environmental variables and taxa composition (Figure 2.7). The first and second axes respectively accounted for 19.52% and 18.30% of the explained variation in community composition. Winter draining, low algal biomass and small waterbody size, with sometimes the absence of fish, were associated with an increased in the abundance of medium and large-sized cladocerans (*Ceriodaphnia reticulata*, *Ceriodaphnia* sp., *Scapholeberis* sp. and *Daphnia* spp.). Higher algal biomass (total chlorophyll *a*), especially of the Greens and Browns spectral groups, usually in the presence of fish were associated with an increase in small rotifers (*Keratella* sp., *Polyarthra* spp., *Euchlanis* spp. and *Plationus patulus*). Shallower waterbodies had communities sometimes dominated by the rotifer *Lecane* sp., whereas deeper waterbodies had communities dominated by the cladocerans Bosminidae spp. and *Diaphanosoma* sp.
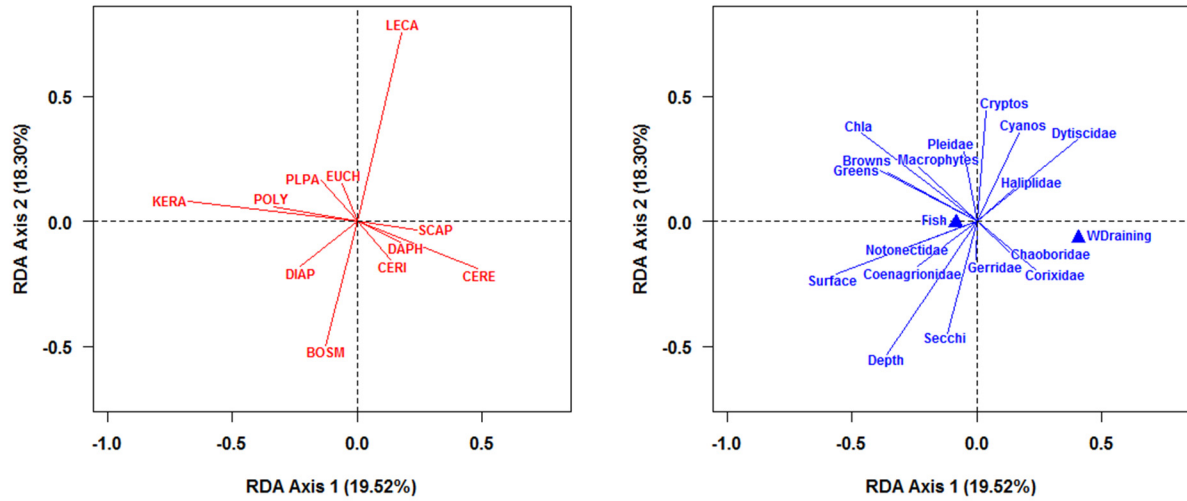
Figure 2.7: Ordination plots of the RDA model describing zooplankton communities and all three sets of environmental variables. Panel a) shows species vectors and panel b) shows environmental variables (vectors for continuous variables and centroids for qualitative variables). The first canonical axis accounted for 19.52% and the second axis for 18.30% of the explained variation. In order to retain only important taxa and improve legibility, only taxa that were well-explained by the analysis and well-represented in the two-dimensional space are represented.

2.5 Discussion

Despite their location in an urban landscape and the consequent predominant presence of anthropogenic stressors, waterbodies in Montreal sustain noticeable amounts of aquatic biodiversity for several zooplankton groups. Indeed, our survey across littoral and pelagic habitats of 18 waterbodies revealed species richness values for each zooplankton group that are close to values found in studies of lakes in Eastern Canada (Pinel-Alloul et al. 1990, Pinto-Coelho et al. 2005, Barnett and Beisner 2007) or the northern United States (Dodson et al. 2005, Larson et al. 2009; see Appendix 2). For cladocerans, the regional pool of 26 species is comparable to values reported in other small lakes and ponds at the regional scale, and is somewhat less than values reported over larger continental scales in northern temperate lakes (Walseng et al. 2006, Pinel-Alloul et al. 2013). Our urban regional pool of 45 rotifer taxa is smaller than the number reported in three summer surveys of 19 waterbodies of a Polish city (Ejsmont-Karabin and Kuczyńska-Kippen 2001) and in lakes of British Columbia and Yukon Territory of Canada (Chengalath and Koste 1987) or of New Zealand (Duggan et al. 2001). However, it is comparable to that observed in ponds of Argentina and Spain (Frutos and Carnevali 2008, Jose de Paggi et al. 2008, Escrivà et al. 2010). Copepods showed the lowest number of species, which is also commonly reported in ponds (Frutos and Carnevali 2008, Jose de Paggi et al. 2008, Escrivà et al. 2010) and natural lakes (Pinel-Alloul et al. 1990). Even though such direct comparisons are hampered by important differences in the number of studied waterbodies, sampling methodology and ecological environments, they still show that urban waterbodies can represent important reservoirs of biodiversity.

We found a lack of agreement between waterbody contributions to regional cumulative species richness (gamma diversity) and among-waterbody variation in community

composition (beta diversity). Waterbodies dominated by a single or few zooplankton species that were mostly absent from or made up a small part of the community composition of other sites, showed high contributions to beta diversity (LCBD indices), even though they contributed little to regional (gamma) species richness. Indeed, out of the five waterbodies which showed sampling units with significant LCBD values, three of these were species-poor sites that were emptied during the winter. In contrast, other waterbodies with species-rich and diverse communities (numerous taxa from different groups and especially littoral taxa) were important contributors to gamma richness, despite the fact that they contributed less to beta diversity. This observation indicates a conservation value of small, species-poor waterbodies that, despite their low species richness, contribute to important variation in community composition between sites. This inverse relationship between regional richness and LCBD indices was found when considering the entire zooplankton community, but was not observed for the cladoceran and rotifer groups individually.

Furthermore, though zooplankton LCBD values differed between waterbodies, partitioning of this value into contributions of zooplankton groups revealed a strong negative relationship between the contribution of individual waterbodies to rotifer and cladoceran beta diversity. Thus, waterbodies contributed to overall zooplankton beta diversity through either rotifers or cladocerans, but not both. This inverse pattern could be the result of the exploitative and interference competition between cladocerans and rotiferan communities (Gilbert & Stemberger 1985, Gilbert & MacIsaac 1989, MacIsaac and Gilbert 1991). Further studies, including a temporal following of these communities in these waterbodies, would be needed to disentangle abiotic constraints from biotic interactions. Nevertheless, there seems to be a strong relationship between cladocerans and rotifer communities. Consequently, to fully assess

zooplankton diversity patterns in these urban waterbodies, all zooplankton taxonomic assemblages should be sampled and have their individual contributions to biodiversity assessed.

Rotifers and cladocerans were the main contributors to regional (gamma) species richness. Furthermore, most of the species with high variation among the waterbodies (high SCBD indices) also belonged to these two taxonomic groups. This result was expected, as reproduction mainly through the asexual mode of parthenogenesis and short generation times enables rotifers and cladocerans to rapidly colonize new environments and develop large, more dynamic populations. Furthermore, they are capable of producing resting eggs, which are resistant to adverse conditions such as drought and freezing, thereby ensuring species persistence in temporary ponds, as well as providing potential dispersal stages that can colonize new waterbodies (Gilbert 1974, Ricci 2001). This contrasts with the life-history traits of copepods, which are obligatory sexual taxa, with longer life cycles, several ontogenetic stages and long-lasting periods of active or dormant diapause. Due to these life-history traits, copepods would require mostly permanent and stable habitats to fully complete their development. Consequently, we expected them to be less common and less abundant than rotifers or cladocerans, which would lead them to having a less important contribution to zooplankton beta diversity.

The littoral zone of waterbodies is recognized as being important for aquatic biodiversity, contributing considerably to species richness in lakes (Walseng et al. 2006, Vadeboncoeur et al. 2011). Our results support this tendency in urban waterbodies, indicating that the littoral vegetated zone should be a region of interest when assessing zooplankton diversity and in conservation plans. In the case of the cladocerans, there may be several

reasons for this observation. It could be that macrophytes in the littoral zone provide a refuge from some predators for "free-swimming" cladocerans under certain conditions (Burks et al. 2001a, Burks et al. 2002). The littoral zone could also represent a more heterogeneous habitat, offering a wider assortment of microhabitats, especially for benthic and "plant-associated" species (DiFonzo and Campbell 1988, Tremel et al. 2000). It is likely that both of these mechanisms are at work simultaneously, leading to greater aquatic diversity in the littoral zone.

In our case, the significant interactions for all diversity metrics would indicate that the direct effects of the littoral zone could not be considered independently of the focal waterbody. The littoral zone of waterbodies could produce sampling units which were equally rich as those of the pelagic zone or remarkably richer, up to more than twice the number of taxa. Similar patterns were also observed with multivariate diversity metrics (Jaccard dissimilarity and Hellinger distance), wherein communities between zones in waterbodies could be quite similar or very different. Lack of community differences between zones in certain waterbodies could be due to the fact that macrophytes did not always form a "belt" around the perimeter of the waterbody. In the most obvious case of Prairies, an extensive degree of coverage by *Ceratophyllum demersum* could have also blurred the distinction between the two zones. However, some waterbodies with less macrophyte cover (Liesse, Beaubien, Jarry) also had relatively undifferentiated communities between the two zones.

The observed community variability within waterbodies could also be related to biotic processes, such as zooplankton patchiness behaviour (Fairchild 1981, Pinel-Alloul 1995). Furthermore, the structural complexity of the littoral zone, based on the architecture of macrophytes and plant type (and not just their overall spatial arrangement) may also be an

important factor. Indeed, within the littoral zone, zooplankton communities can differ between habitat types (Tremel et al. 2000) and taxa can show an affinities for specific macrophyte species (Kuczyńska-Kippen 2009a and 2009b). Part of this affinity can be due to the architecture of plants and their leaves, with macrophytes possessing more finely dissected leaves providing a better refuge against visual predators. These types of plants should support more abundant and diverse zooplankton communities. Biodiversity loss should therefore be expected when macrophytes are removed, which completely removes a structural component of the environment and would have different effects on the community if macrophyte species harbour particular zooplankton taxa.

Zooplankton beta diversity and community structure in our urban waterbodies were affected by a range of environmental factors, as is also the case for non-urban lakes (Pinel-Alloul et al. 1995, Beisner et al. 2006). In the RDA, environmental variables associated with bottom-up (morphometry, water quality and nutrient enrichment) and top-down forces (macroinvertebrate predation), as well as management practices, all influenced our urban zooplankton communities. In particular, the management practice of routinely draining waterbodies during winter affected zooplankton communities by increasing the relative abundance of medium and large-bodied cladocerans in these environments. All the taxa in this group of cladocerans have quite high SCBD values and this is likely the cause for the high and significant LCBD values that these waterbodies show. The persistence of these communities within urban waterbodies, despite habitat loss, may be attributable to their capacity to produce dormant or quiescent stages that are able to withstand adverse conditions and allow habitat recolonizing (Hairston Jr. 1996, Radzikowski 2013). However, though the practice of draining ponds during winter may resemble the drying out of natural temporary ponds during summer,

it is not actually that similar. During winter draining, the bottom of the urban ponds is also sometimes cleaned before they are filled again, generally removing all water and sediments containing the original community. In such cases, re-colonization must occur from other waterbodies, a process that is aided by the presence of dormant stages such as resting eggs that can be transported by wind, streams or vertebrates associated with several waterbodies.

Despite the fact that planktivorous fish can directly affect zooplankton through selective predation, but also indirectly through bioturbation and resuspension of sediments in shallow waterbodies (Scheffer et al. 2003), the RDA model did not show a strong effect of the presence of fish on the zooplankton communities. Most of our studied waterbodies contained fish and, in particular, cyprinids (sometimes carps) whose foraging activity can increase resuspension of sediments. More fish-free waterbodies would be needed to verify any fish effect. Macroinvertebrate predators of zooplankton were also present and affected zooplankton communities (Burks et al. 2001b, Gilbert and Hampton 2001, Hampton and Gilbert 2001). In the fishless waterbodies, water boatmen (Corixidae) and tiger beetles (Dytiscidae) were common. In these ecosystems, invertebrates likely acted as top predators affecting zooplankton directly and indirectly through the food web (Cobbaert et al. 2010).

Zooplankton communities in temporary waterbodies (Mahoney et al. 1990, Sahuquillo and Miracle 2010) as well as those of permanent lakes (Hairston Jr. et al. 2000) can change through time. Consequently, our estimates of species richness and diversity, based on a single sampling campaign, might have missed species appearing earlier or later during the summer and should thus be considered as lower bounds of zooplankton diversity in urban waterbodies. Waterbodies are part of the urban landscape, which means that they will be directly influenced by anthropogenic effects and management practices, as shown by our study of zooplankton

communities. In addition to serving an important aesthetic purpose in cities, waterbodies in cities can also act as reservoirs of urban biodiversity. Our study has shown that they contain important and varied amounts of diversity. Management practices should ensure the maintenance of both gamma and beta diversity in urban watersheds. Policies favouring a large diversity of permanent and temporary habitats with vegetated littoral zones should thus be incorporated in conservation plans.

2.6 Acknowledgements

Chapter 3

Phylogenetic diversity and its conservation in the presence of phylogenetic uncertainty:

A case study for cladoceran communities in urban waterbodies

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3.1 Abstract

The need to protect and preserve biodiversity is a pressing issue and conservation projects based on solid foundations are invaluable. Urban waterbodies constitute unique freshwater environments that can harbour noticeable biodiversity, but various causes threaten this biodiversity, making it imperative to be able to determine sites or groups to sites to prioritize in biodiversity conservation. Knowledge of species evolutionary history can serve as a tool to help guide conservation projects on the basis of evolutionary heritage. We used communities of Cladocera (Crustacea, Branchiopoda) in urban waterbodies to identify which sites should be prioritized for phylogenetic diversity conservation, as well as to evaluate the consequences of phylogenetic uncertainty for identifying sites for conservation priority. Phylogenetic trees were inferred using DNA sequences from two mitochondrial genes. Using results from Bayesian analyses, we considered the effect of uncertainty in the phylogenetic tree on phylogenetic diversity (PD) estimation and the comparison of phylogenetic diversity among sites. When phylogenetic uncertainty is taken into account, the conservation value of individual sites becomes uncertain and several potential comparisons between sites should not be given any support. Our study highlights the fact that, in the presence of phylogenetic uncertainty, prioritization ranks become unresolved and prioritization should thus be determined more cautiously. Therefore, variability in the phylogenetic estimates should be consistently considered and integrated into estimates of phylogenetic diversity and conservation decisions to avoid making suboptimal choices.

Keywords: Phylogenetic diversity, evolutionary heritage, phylogenetic uncertainty, site conservation, cladoceran diversity, urban waterbodies

3.2 Introduction

The expansion of the human population has led to pronounced impacts on ecosystems and a remarkable decrease in biodiversity. It is therefore imperative to be able to provide and evaluate biodiversity conservation strategies before more diversity is lost. However, despite the fact that they may be most affected by human disturbances, the evaluation and conservation of invertebrate taxa is not well developed (New 1993, Strayer 2006, Vicente 2010). In freshwater environments such as ponds or wetlands, human activity can exert a considerable influence. However, despite strong anthropic effects and perturbations, urban ponds can represent important reservoirs of biodiversity (Hassall 2014). Within these habitats, species belonging to the taxa Cladocera (Crustacea, Branchiopoda) contribute to a large portion of the overall biodiversity (Pinel-Alloul and Mimouni 2013, Mimouni et al. 2015). These micro-crustaceans are one of the most important invertebrates for ecosystem and food web functioning. They occupy a central place in aquatic food webs and are thus key actors, playing a fundamental role in the flow of nutrients from algae and bacteria to higher trophic levels. Their population dynamics and community composition reflect changes in algal prey and predation by fish and invertebrates (McQueen et al. 1986, Finlay et al. 2007, Gélinas and Pinel-Alloul 2007).

While many cladoceran species have been reported to have wide distributions, this is largely a result of morphological stasis and large degrees of morphological character variation. However, based on molecular studies, many species have shown divergent lineages indicating regionally distributed clades, including *Sida crystallina* (Cox and Hebert 2001), *Chydorus sphaericus* (Belyaeva and Taylor 2009), *Polyphemus pediculus* (Xu et al. 2009) and *Leptodora kindtii* (Xu et al. 2011). Doubts about the cosmopolitanism of cladoceran taxa have also been

raised on the basis of detailed morphological analysis (Frey 1973 and 1980). Consequently, views on cosmopolitanism for Cladocera have changed over the years (Frey 1982, 1987 and 1995), and newer frameworks consider high levels of endemism and cryptic species complexes. In light of these findings, conservation plans for urban aquatic habitats will also need to be modified to place a larger emphasis on preservation of local biota.

In addition to aiding taxonomic and biogeographical studies, molecular data can aid conservation studies by providing knowledge of species' evolutionary history (Erwin 1991, Soltis and Gitzendanner 1999, Bowen 2002). In conservation biology, ranking the importance of species or areas requires making informed choices. The Noah's Ark Problem (NAP, Weitzman 1998) is a theoretical model that seeks the most cost-effective way to preserve biodiversity, and can be used to determine prioritization. Within this model, proposed conservation projects will affect a species' survival probability for a given cost. Following this, a ranking criterion for species can be constructed as the product between the ratio of these values and a two-part, species-specific sum. The first part of this sum is highly anthropocentric, being a subjective value of how much we value a species (e.g. on aesthetic, commercial or religious bases, Metrick and Weitzman 1998). The second part of this sum is more objective, describing the distinctiveness of the species. In this case, the notion of molecular diversity is an attractive one, because it is based on a "common yardstick" (Avise 1994) of genetic material, which all living things share and may be used to guide prioritization based on an objective and quantitative basis. The model uses values such as the increase in probability of survival for each species based on enabling the project and the cost of each project, which allows for the formulation and consideration of alternative scenarios. For aquatic communities, the cost and effectiveness of projects aiming to preserve diversity and

ecosystem integrity can be difficult to estimate on a by-species basis. In this study, we shall consider the issue of conservation and ranking of sites, wherein the following assumptions hold: every species has the same utility, every site has the same cost to preserve, conservation preservation projects always ensure the survival of a site's community, and species within non-protected sites will go extinct with certainty. Although this can correspond to an extreme setting of the project, this set of conditions likely applies best to urban aquatic ecosystems, wherein entire habitats can be completely eradicated or radically modified due to urban planning and human disturbances, leaving little time for communities to react or adapt.

Ponds and small waterbodies represent biologically interesting environments that can represent non-negligible sources of biodiversity as they often contain several rare or unique species and can contribute notably to landscape diversity (Oertli et al. 2002, Wood et al. 2003, Williams et al. 2003). However, these waterbodies and their biodiversity face a number of threats (Brönmark and Hansson 2002, E.P.C.N. 2007, 2008). Furthermore, increasing pressure due to the necessity of land for urban space and agricultural intensification have led to a considerable decline in the number ponds in some areas (Wood et al. 2003, Hassall 2014). For waterbodies located in urban environments, human population density and the ensuing anthropogenic stressors may also have strong impacts. In these cases, inappropriate management of waterbodies or their surrounding environment can affect the communities they harbour. Therefore, it is imperative to be able to obtain an idea of the conservation values of urban ponds, but also to be able to identify the most important sources of urban biodiversity towards which to prioritize conservation efforts.

The main purposes of the study were to establish a ranking of waterbodies based on the evolutionary history they contain and explore how to choose groups of waterbodies in order to

maximize phylogenetic diversity over a landscape. DNA sequences from two mitochondrial genes were used to infer phylogenetic trees using Bayesian methods. We made use of the Bayesian method of phylogenetic inference as its biological assumptions and mathematical bases are explicit, which facilitates the use of results in further analyses. Indices of phylogenetic diversity are computed for cladoceran assemblage data for a set of waterbodies spanning a variety of environmental conditions. Furthermore, there seems to be somewhat of a disconnection between the probabilistic nature of phylogenetic inference and the application of its results to biodiversity conservation. Indeed, it has been noted that further effort should be given to the uncertainty surrounding phylogenetic tree and branch length estimation, and its impact on phylogenetic diversity (Faith 2013). Consequently, we also focused on the impact that uncertainty in the phylogenetic inference process has on the issue of biodiversity preservation. We address this issue by incorporating phylogenetic uncertainty by computing indices of phylogenetic diversity on the posterior distribution of trees. From this collection of phylogenetic diversity values, 95% credible intervals for the phylogenetic diversity of a site and for the difference in phylogenetic diversity between a pair of sites are determined. These intervals allowed estimation of phylogenetic uncertainty and made comparisons of phylogenetic diversity between sites possible. They also provided a way to determine the extent to which uncertainty in the inference of the phylogenetic tree would affect prioritization choices.

3.3 Methods

3.3.1 Study sites and zooplankton sampling and analysis

In the months of June, July and August of 2011, nineteen waterbodies of various types (including permanent and temporary ponds, as well as three wetlands), distributed over the city of Montreal (QC, Canada) (45.46 - 45.69ºN; 73.50 - 73.90ºW), were sampled to evaluate the diversity of zooplankton assemblages in urban environments. The waterbodies were selected to represent the range of environmental features of aquatic habitats encountered across the waterbodies in the entire city.

A multi-scale field sampling was applied, sampling both among waterbodies and within waterbodies. At each month, the littoral and pelagic zones of each waterbody were sampled separately by randomly choosing three sampling points in the littoral zone, along with three pelagic points in the open-water area directly in front of these, resulting in a total of six sampling points per waterbody. Cladoceran organisms were sampled at each sampling point from a small anchored boat using a 3 L bucket that was dipped ten times to arm's length in surface waters. The 30 L total water sampling unit was subsequently filtered through a 54 µm mesh size plankton net. Retained organisms were first narcotized with carbonated water and fixed in pure formaldehyde.

Zooplankton were kept in formaldehyde for approximately six months to fix the organisms and then transferred to a 75% ethanol and 5% glycerol solution to avoid desiccation, being concentrated into 25 mL scintillation vials. One quarter of each well-mixed zooplankton sampling unit was taken using a pipette with a large-mouthed tip, transferred to a Ward counting wheel (Ward 1955), enumerated under a Leica Wild M3B stereomicroscope and identified under a Wild Heerbrug microscope. Cladoceran taxa were identified to the

finest possible taxonomic resolution (species and genus) using the appropriate keys (Brooks 1959, Korovchinsky 1992, Smirnov 1992 and 1996, Hebert 1995). Occurrences from all the sampling units obtained for all months were combined into a single representative sampling unit for each waterbody in order to account for some of the temporal and within-site variation.

3.3.2 Sequence acquisition and phylogenetic inference

Sequences for recorded species and several other cladoceran taxa were obtained from the GenBank public repository and sequence database (Benson et al. 1997). The sequences used in this study consisted of mitochondrial sequences for cytochrome oxidase subunit I (COI) and 16S ribosomal RNA (16SrRNA). As in deWaard et al. (2006) the malacostracan *Anaspides tasmaniae* was used as the outgroup to root the trees. We also used sequences from several species belonging to the other Branchiopod taxa, so as to have more than one outgroup. These included sequences corresponding to the taxa Anostraca, Notostraca, Laevicaudata and Spinicaudata. Sequences for the clam shrimp *Cyclestheria hislopi* were also included, owing to its close affinity with Cladocera. The list of species and GenBank accession numbers for the sequences used are submitted in Appendix 3.

Cytochrome oxidase subunit I sequences were aligned using the software MUSCLE v3.8.31 (Edgar 2004) with the default options. Third codon positions were tested for substitution saturation (Xia et al. 2003, Xia and Lemey 2009) in the software DAMBE v5.3.36 (Xia 2013). These proved to be quite saturated and were thus not considered in the analysis. 16S ribosomal RNA sequences were aligned with the software MAFFT v7.220 (Katoh and Standley 2013) using the E-INS-i option (Katoh and Toh 2008). Following alignment, sequences were visually inspected for any evident alignment errors and had their trailing ends cropped off to minimize the amount of missing data. Alignments were further processed using

the software Gblocks 0.91b (Castresana 2000, Talavera and Castresana 2007) to remove ambiguous portions of the alignments.

Data partitioning and model selection are important aspects of phylogenetic inference. Consideration of data partitioning and the rate of evolution between partitions affects not only likelihood values (Yang 1996), but has also been shown to affect other important aspects of phylogenetic inference such as bipartition posterior probability (Lemmon and Moriarty 2004, Marshall et al. 2006, Brown and Lemmon 2007) and branch lengths as well. In diversity studies, whose primary interests are topology and branch lengths, these are essential as they are bound to affect phylogenetic diversity values. Selection of the optimal partitioning scheme and best-fitting substitution model was carried out using PartitionFinder v1.1.1 (Lanfear et al. 2012), considering COI by codon position and 16SrRNA as a single subset. All of the most commonly used submodels of the GTR family of models (Lanave et al. 1984, Tavaré 1986) were considered. We included models with rate heterogeneity as modeled by a proportion of invariable sites (Hasegawa et al. 1985, Reeves 1992) or rates following a gamma distribution with an expected value of one (Yang 1993), but not both, as correlations between the parameters can lead to poorly behaved likelihood surfaces and a difficulty to estimate both parameters accurately (Sullivan et al. 1999, Yang 2006). Selection was based on the second-order value of Akaike's an information criterion with correction for small samples (Akaike 1974, Hurvich and Tsai 1989).

Bayesian inference of phylogeny was carried out using the software MrBayes v3.2.5 (Ronquist et al. 2012) using 2 independent runs of 10 million generations. We used a modified version of MrBayes v3.2.5 which can use the compound Dirichlet priors for branch lengths (Rannala et al. 2012, Zhang et al. 2012). Absence of apparent lack of convergence was

assessed using a variety of methods. Trace plots of continuous parameters were visually inspected for an absence of apparent trend and effective sample size were verified in Tracer v1.6 (Rambaut et al. 2014). For topology, a pairwise posterior probability plot was obtained using the graphical convergence exploration tool AWTY (Nylander et al. 2008). The maximum clade credibility (MCC) tree was determined using TreeAnnotator v1.8.2 (Rambaut and Drummond 2013) and drawn using FigTree v1.4.0 (Rambaut 2011).

3.3.3 Phylogenetic diversity measure

There are different ways to define phylogenetic diversity, each with its own calculation and implications for diversity (Vellend et al. 2010). We determined phylogenetic diversity (PD) as the sum of edges on the phylogenetic tree connecting the considered community, as defined by Faith (1992). We included the root of the tree in PD, as it represents an integral part of the evolutionary history of the studied taxa (Faith and Baker 2006, Faith 2006). This index has the most direct interpretation as being the evolutionary history of the considered taxa and is appropriate for conservation-based comparisons, as the evolutionary history of the considered species is the value of interest. Additionally, it is an established index with a large enough body of literature regarding its computational and combinatorial aspects (Steel 2005, Hartmann and Steel 2006, Moulton et al. 2007, Faith 2013). For computation of PD on on specific tree, the MCC tree was used.

Under specific conditions, phylogenetic diversity can be maximized using a greedy algorithm (Steel 2005, Hartmann and Steel 2006). However, region preservation of phylogenetic diversity, the preservation of the phylogenetic diversity within geographically delimited regions, each with their own fauna/flora is an NP-hard problem (Moulton et al. 2007). In this case, the composition of each individual site and the degree of nestedness of

species assemblages will affect results. Owing to the modest number of waterbodies sampled (19 sites), considering each and every one of the $\binom{n}{k}$ possible combinations of k regions is feasible. Computation of PD for every k subset of the 19 sites was performed and the range of obtained values was considered to evaluate how conservation decisions would affect PD preservation.

3.3.4 Incorporating phylogenetic uncertainty in PD estimation

There is a growing need to reconcile the probabilistic nature of phylogenetic inference and the diversity indices that can be derived from it. Incorporation of the phylogenetic uncertainty regarding topology and branch-length estimation would be useful for PD (Faith 2013). An obvious and direct way to construct a modified version of PD that takes into account uncertainty in the tree would be to weigh each edge on the tree by its support (e.g. boostrap proportions, posterior probability). Although this method seems straightforward, certain questions may arise. The first of these relates to which topology should be considered. Indeed, following the estimation of phylogenetic uncertainty, the collection of trees would need to be summarized into a consensus tree, reflecting points on which all the trees agree. This tree is usually a majority-rule consensus tree, which may be different from any individual estimated tree. Furthermore, the consensus tree is most often a cladogram, without branch lengths, or for which branch lengths are difficult to define. While certain methods can estimate branch lengths for consensus trees, including Felsenstein's median branch length tree (2004) or the Bayesian majority-rule consensus tree, there is a debate as to whether consensus trees may represent optimal trees (Miyamoto 1985, Barrett et al. 1991, Holder et al. 2008). One could also project the support values on the tree to be used in PD analyses, but with caution,

depending on the level of disagreement between all the generated trees and the tree considered for PD estimation.

However, this method would only assess the topological corroboration of the considered tree estimate and would discard information on branch lengths. In other words, we could only get an idea of how uncertainty in the topology affects our estimates by comparing the values of this modified PD index with the regular one. Low support for branches should translate into lower values of this modified index of PD than for the regular index. What would be needed is a method that could give the range of values that PD could take, which would give a more straightforward interpretation and could help in applications of biodiversity conservation. In light of these considerations, we computed PD separately on each tree in the posterior distribution of trees, considering the range of both raw values and ranks observed.

The distribution of PD obtained from the posterior distribution of trees could also be the posterior distribution of PD itself and intervals derived from it could be interpreted as credible intervals (Lewis and Lewis 2005). Comparisons of PD between sites were made by considering the difference in PD values between sites. This captures the fact that both PD values were computed on the same tree and are therefore not independent.

The majority of statistical analyses were carried out using the R statistical language (R Development Core Team 2012), using functions from the packages *ape* (Paradis et al. 2004), and *picante* (Kembel et al. 2010).

3.4 Results

3.4.1 Cladoceran species richness and community composition

Twenty-four cladoceran taxa were inventoried in the sampled waterbodies. These included 1 taxon belonging to the family Bosminidae, 11 to Chydoridae, 6 to Daphniidae, 1 to Ilyocryptidae, 1 to Leptodoridae, 1 to Macrothricidae, 1 to Polyphemidae and 2 to Sididae. Species richness varied widely between sites, ranging from species-poor sites with 2 species to species-rich sites with 16 species (Table 3.1). Taxa presence-absence patterns were extremely variable, with more than half of the taxa (15 taxa) being present in less than 10 sites. Several taxa were quite rare as four taxa appeared in three sites, three in two sites and four in only a single site (Appendix 4).

Table 3.1: Estimates of species richness (SR) and phylogenetic diversity (PD) for urban cladoceran communities based on the MCC tree and 95% quantile-based intervals of PD according to the posterior distribution.

	SR	PD	Posterior
Cygnes	16	1.494	[1.419, 1.876]
Angrignon	12	1.088	[1.080, 1.463]
LCastors	12	1.073	[1.140, 1.543]
JBNenuphars	14	1.061	[1.133, 1.538]
JBAlgues	13	1.060	[1.058, 1.462]
Bizard	13	1.022	[1.048, 1.435]
Heritage	10	1.017	[0.965, 1.339]
Lacoursiere	12	1.004	[1.016, 1.393]
Brunante	9	0.884	[0.907, 1.265]
Beaubien	9	0.852	[0.859, 1.212]
Lafontaine	8	0.828	[0.816, 1.144]
Jarry	8	0.797	[0.852, 1.184]
Battures	8	0.741	[0.741, 1.063]
Liesse	8	0.719	[0.708, 1.016]
Pratt2	6	0.702	[0.671, 0.968]
Prairies	7	0.693	[0.662, 0.953]
MCastors	6	0.679	[0.685, 0.997]
Centenaire	6	0.628	[0.609, 0.923]
RMontigny	2	0.302	[0.305, 0.497]

3.4.2 Sequence acquisition and phylogenetic inference

COI sequences aligned quite easily and showed no insertion-deletion events. The final COI data-matrix was 426 bp long after removal of saturated third codon positions. However, aligned 16SrRNA sequences presented several regions with gaps and possibly ambiguous alignment of nucleotides. The software Gblocks removed 219 bp out of the originally 528 bp long alignment, yielding a 309 bp long alignment. The final mitochondrial DNA (mtDNA) data-matrix consisted of 47 taxa and was 736 bp long.

The optimal partitioning scheme, as determined by AIC$_c$ values, was by codon position and by gene, in which each codon position of the COI gene and the 16SrRNA gene were modeled by separate models. Within this partitioning scheme, first positions of the COI gene were modeled using a SYM+Γ model and second positions of the COI gene and the 16SrRNA gene was modeled using separate GTR+Γ models.

Visual observation of trace plots of the log-likelihood and various parameters indicated that the runs for Bayesian analyses did not show signs of absence of convergence after removal of the burnin. Using AWTY, pairwise posterior probability plots also showed high correlations between the two runs, indicating no noticeable lack of convergence.

3.4.3 Phylogenetic relationships among the Cladocera

The MCC tree is shown as Figure 3.1. The analysis strongly supported the clade Cladoceromorpha, which is the association of the taxa Cladocera and Cyclestherida (Ax 2000). The monophyly of Cladocera and its closeness with the clam shrimp *Cyclestheria* have already been reported in several studies (Spears and Abele 2000, Braband et al. 2002, deWaard et al. 2006, Stenderup et al. 2006). Even though the analysis recovered the four main

cladoceran taxa of Anomopoda, Ctenopoda, Haplopoda and Onychopoda, the associations between these taxa received little support. Furthermore, lower level resolution was variable, as support for each of these groups and the species they contain was quite variable. Consequently, phylogenetic relationships between Cladocera determined from mtDNA sequences are close to currently established taxonomy, but show considerable amounts of uncertainty for intermediate levels of resolution.
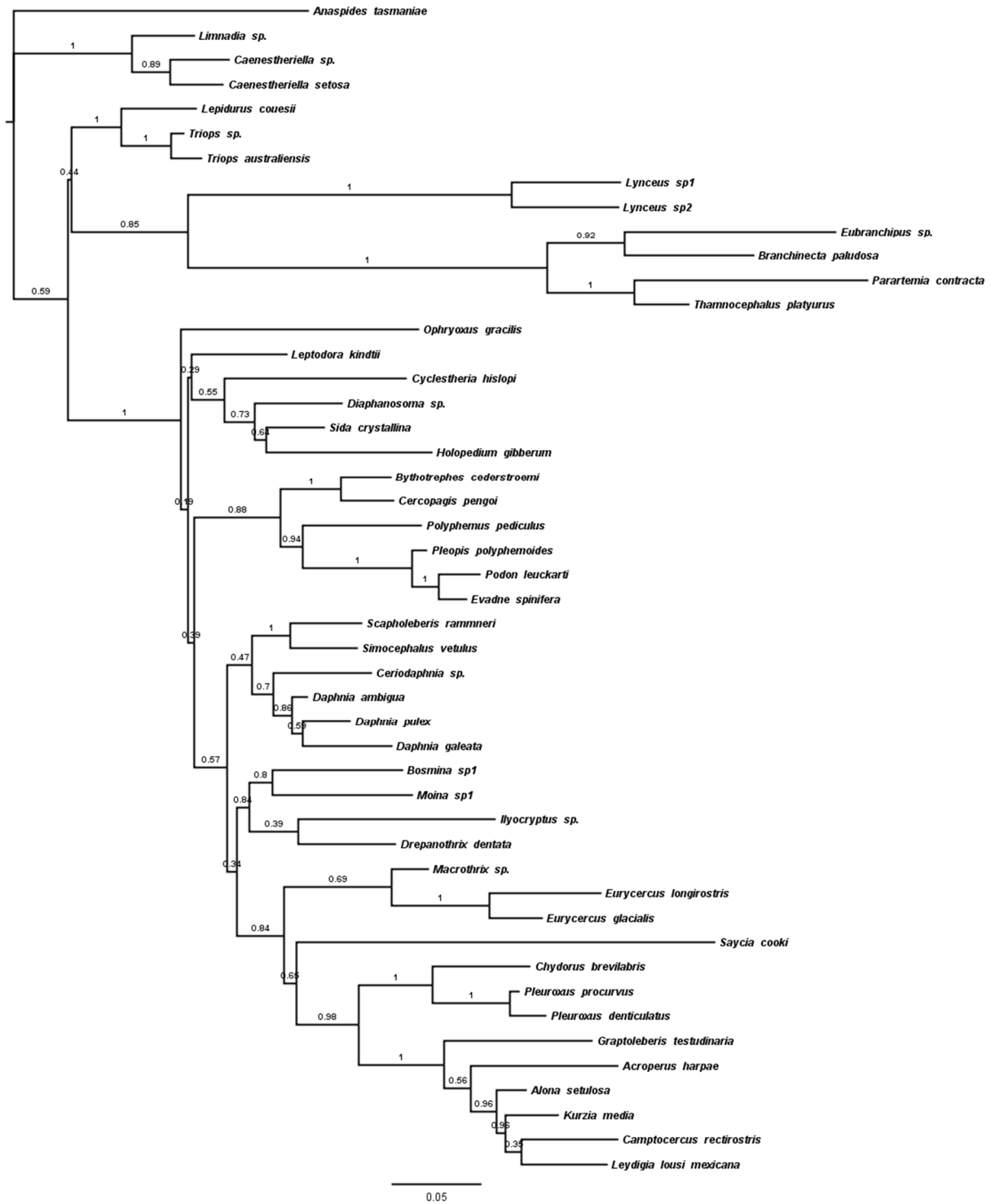
Figure 3.1: Maximum clade credibility mtDNA gene-tree for the cladoceran taxa. The posterior probabilities of each split are indicated above it. The scale bar indicates the expected number of substitutions per site.

3.4.4 Site selection and biodiversity preservation

The sampled waterbodies differed in their phylogenetic diversity as PD values ranged from 0.30 to 1.49 (Table 3.1), making the difference between the best choice and the worst choice for the preservation of a single site equal to 1.19. This result considers only a single site to preserve. However, differences between the best and worst combinations of sites to preserve to maximize PD persisted up until all sites were preserved (Table 3.2). It was only at this point that both choices preserved the same amount of PD, which was expected as there can only be a single combination of n out of n objects. When always selecting the combination of sites that maximizes PD, the amount of PD that is preserved increases rapidly before reaching the maximum value of 1.90 at five sites. Contrary to this, suboptimal choices were present for all numbers of sites and the maximal value of PD attained only when all 19 sites are considered when the worst combination of sites is taken. This would imply that even when almost all sites are preserved, as many as eighteen, there is at least one combination that could be viewed as suboptimal to PD preservation. Visual observation of sorted barplots for all combination of sites showed the range of values between these extremes (Figure 3.2). These showed a peak at the maximal value of PD for several combinations followed by a strong slope, before finishing abruptly. As the number of sites considered increases, these aspects are gradually less pronounced, as the peak is less distinct, the slope is flatter, and the end is not as abrupt.

Table 3.2: Minimum amount of PD preserved (MinPD), maximum amount of PD preserved (MaxPD), average amount of PD preserved (AvgPD), median amount of PD preserved (MedPD), standard deviation of all PD values (Std), number of combinations of PD (NComb) and number of optimal combinations of PD (NOpt) for each number of sites that can be preserved.

Number of Sites	MinPD	MaxPD	AvgPD	MedPD	Std	NComb	NOpt
1	0.30	1.49	0.88	0.85	0.25	19	1
2	0.68	1.77	1.11	1.07	0.20	171	1
3	0.78	1.84	1.24	1.20	0.20	969	2
4	0.81	1.89	1.34	1.29	0.21	3876	4
5	0.87	1.90	1.42	1.37	0.21	11628	6
6	0.94	1.90	1.49	1.45	0.21	27132	75
7	1.00	1.90	1.55	1.51	0.20	50388	434
8	1.04	1.90	1.60	1.56	0.20	75582	1541
9	1.07	1.90	1.64	1.68	0.19	92378	3751
10	1.10	1.90	1.68	1.71	0.18	92378	6622
11	1.12	1.90	1.72	1.79	0.17	75582	8745
12	1.23	1.90	1.75	1.84	0.16	50388	8778
13	1.25	1.90	1.78	1.85	0.14	27132	6732
14	1.34	1.90	1.81	1.85	0.13	11628	3927
15	1.38	1.90	1.83	1.89	0.11	3876	1716
16	1.39	1.90	1.85	1.90	0.09	969	545
17	1.51	1.90	1.87	1.90	0.07	171	119
18	1.69	1.90	1.89	1.90	0.05	19	16
19	1.90	1.90	1.90	1.90	NA	1	1
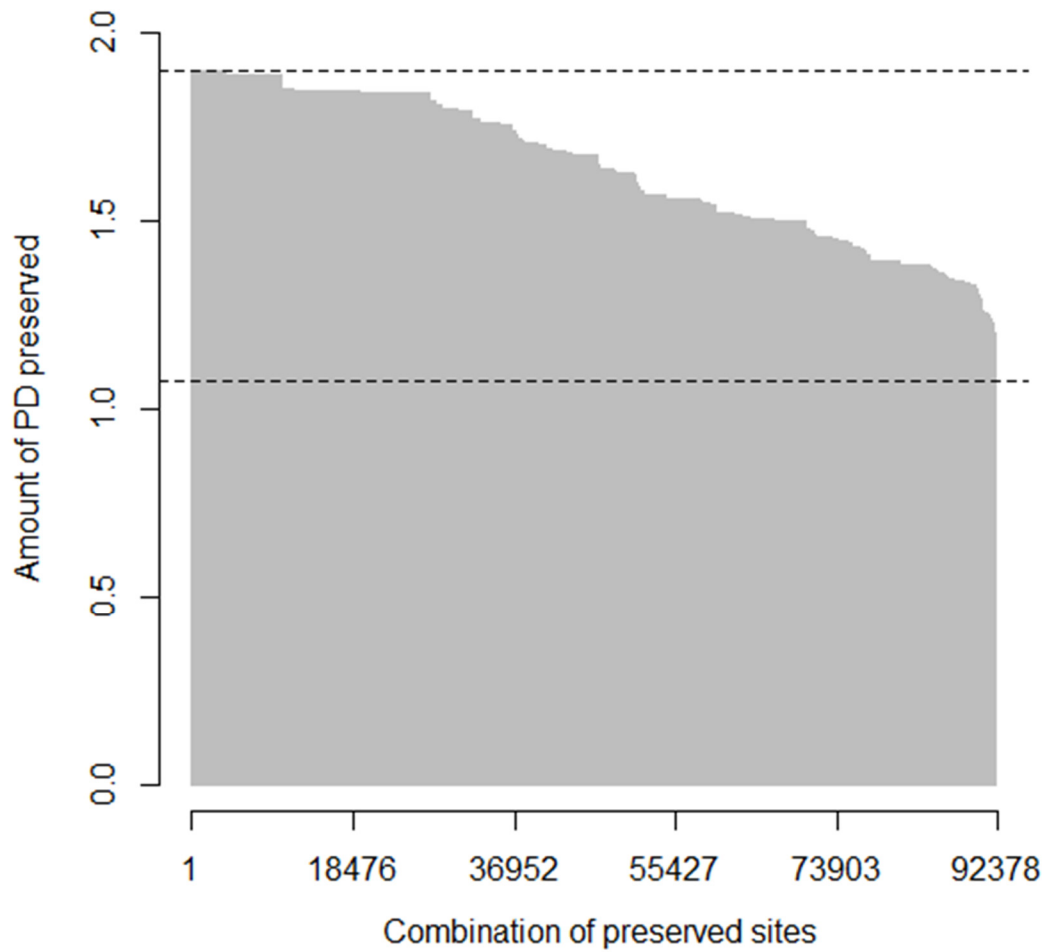
Figure 3.2: Barplot showing the distribution of the amount of PD conserved for all 92 378 possible combinations of 9 sites out of the 19. Values are sorted in decreasing order. The dashed bars in each barplot represent the maximal and minimal values of PD preserved.

The optimal set of sites for PD preservation in subsets is not necessarily the one that would be found with a greedy algorithm, which would proceed by computing PD values for all sites and add sites sequentially starting from the 1st until a subset of size k is attained, would obtain. Indeed, for $k = 2$, the combination of the 1st and 3rd sites maximized PD (numbers being single site PD ranks). This is due to the fact that the 1st and 2nd sites shared several taxa and thus their combination was poorer in PD than one that would be obtained by combining sites with more distinct communities. Furthermore, for $k = 3$, there are two equally optimal combinations of sites that maximize PD, indicating that several combinations of sites can lead to maximizing PD.

3.4.5 Phylogenetic uncertainty and PD comparison

The intervals of PD for each waterbody obtained from the posterior distribution of trees were quite different from one another both in location and in the range of values they bounded (Table 3.1). Quantile-based intervals from the Bayesian posterior distribution of trees showed endpoints that covered a broad range of values, indicating an appreciable amount of uncertainty in phylogenetic reconstruction.

By considering a credible interval for the difference in PD values, a comparison can be made between the PD values of the different waterbodies. For each tree in the posterior distribution, the difference in PD values for two sites was calculated, thus taking into account the fact that these PD values were paired across trees. For the 1st and 2nd waterbodies, the 95% interval was $[0.285, 0.478]$. There is therefore support for stating that the 1st site has a higher PD value than the 2nd site. On the opposite, when comparing the 2nd and 3rd sites, the 95%

interval was $[-0.176, 0.030]$. Contrary to the first case, there is no support for stating that the 2nd site has a higher PD value than the 3rd site.

The bulk of these results can be neatly summarized by transforming raw values into ranks and considering 95% quantiles (Figure 3.3). These intervals show the rank values of sites across of trees, which take into account the order of values. Indeed, due to the fact that the PD values are paired across trees, this notion should be taken into account. In this figure, if the intervals for a pair of sites do not overlap, then we have support in stating that these two sites have different PD values and conservation prioritization can be justified. The result that the 1st site contains more PD than the 2nd, but that the 2nd does not contain more than the 3rd can be seen here, as intervals for the former do not overlap, but they do for the latter. It can also be seen that, if the question were reversed and we were seeking the site with the least amount of PD to discard, then we would be supported in deciding on the 19th site, as its interval does not overlap with the 18th site. Furthermore, it can be seen that, when phylogenetic uncertainty is taken into account, many of the comparisons between sites would prove to be non-significant and the ranking as a whole is less authoritative. It should be noted that there is a loss of information when going from raw values to ranks and that by doing so, any idea of magnitude of the difference between PD values is lost.
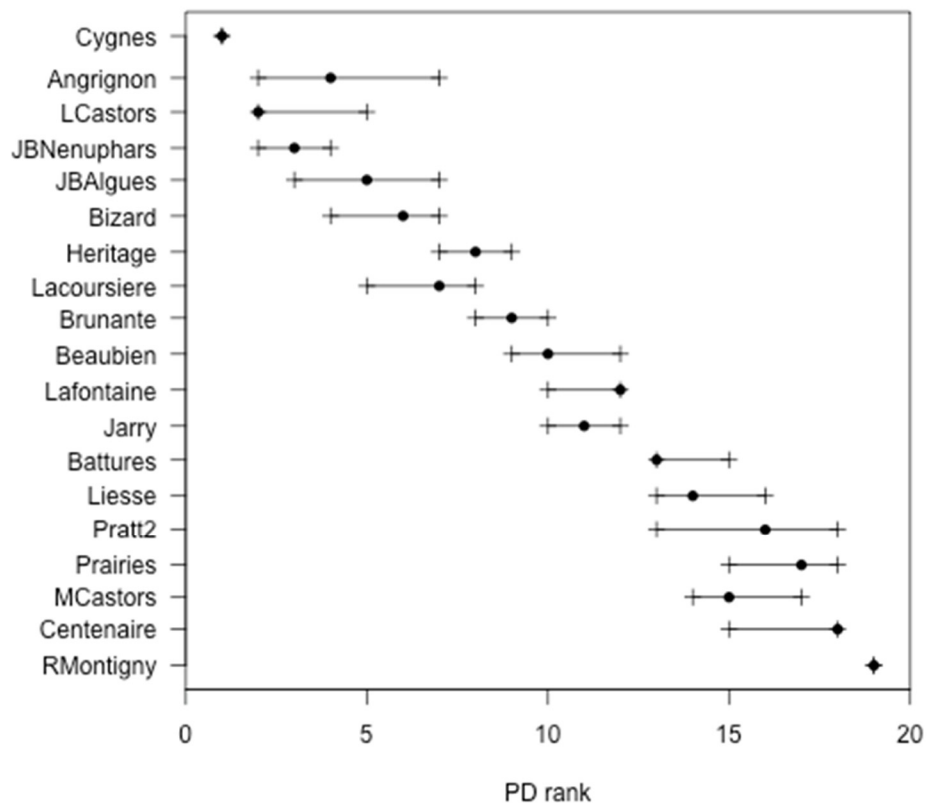
Figure 3.3: Median and 95% intervals of the PD rank for the 19 sites sampled for cladoceran communities for the Bayesian posterior distribution of trees.

3.5 Discussion

Conservation policies and phylogenetic diversity

Ponds and other small waterbodies are common freshwater ecosystems. Although they may be small in size, they can contain several rare or unique species and can contribute notably to landscape diversity (Oertli et al. 2002, Wood et al. 2003, Williams et al. 2003). Within urban environments, these waterbodies and their communities respond to various ecological factors and anthropic stressors, but also park maintenance agents and citizen's attitudes and perception, which may affect their management and viability. Despite the presence of human activities and stressors, urban waterbodies can contain noticeable amounts of zooplankton biodiversity and are should not necessarily have poor biodiversity (Langley et al. 1995, Ejsmont-Karabin and Kuczyńska-Kippen 2001, Mimouni et al. 2015). Consequently, they may represent important reservoirs for urban zooplankton biodiversity. It is therefore imperative to be able to assess their biodiversity value and evaluate conservation plans.

However, increasing pressure due to the necessity of land for urban space and agricultural intensification have led to a considerable decline in the number ponds in some areas of the world (Wood et al. 2003, Hassall 2014). In Montreal, waterbodies are more or less abundant, but they can suffer from poor management practices, which can threaten their communities. Indeed, ponds can be removed from the landscape through various processes, such as infilling, habitat change or lack of maintenance (for ponds that would dry out unless supplied with water). Furthermore, management practices, such as the act of emptying and cleaning the waterbody can affect zooplankton communities (Mimouni et al. 2015). These phenomena can weaken communities or can completely destroy them. For example, following sampling, we noted that the waterbody LCastors had been drained and redesigned in its

entirety. Sediments and organic matter at the bottom were removed in order to remodel the waterbody. However, this very likely removed almost all dormant stages of zooplankton taxa, making it such that the current biodiversity for this waterbody is most likely lower than the one reported in this paper. Consequently, there is a real need not only to determine the biodiversity potential of the various urban ponds, but also enforce practices that do not negatively affect it.

Selection of which sites are to receive greater conservation focus affects how much phylogenetic diversity is preserved. However, it is important to properly guide conservation projects to avoid making suboptimal choices. While the number of subsets k of n sites can be enumerated by the binomial coefficient, it becomes difficult to consider every combination beyond a certain number of sites. For the specific case of region conservation, algorithms that can find the optimal solution can be difficult to find (Moulton et al. 2007). Consideration of the differences between the best and worst combinations of sites revealed that suboptimal choices were always present. If the best choices are always followed, PD for urban cladoceran communities can be maximized using only a few sites. Even though this result should not imply that only these sites should be preserved, it does show that judicious selection of which sites to prioritize can lead to preserving a maximal amount of diversity in a complicated problem.

When sorted, the series of combinations of waterbodies to preserve showed a few optimal values, followed by a moderate decrease and finally a few very suboptimal values. As the number of sites that can be preserved increased, these patterns tended to disappear, and the difference between the optimal and less-than optimal choices tended to decrease. This may indicate that, as the number of sites that can be preserved increases, the number of ways that a

bad choice can be made declines. However, this may not be a general rule, since all of these features are undoubtedly dataset-dependent, being influenced by aspects such as the degree of complementarity between reserves and the shape of the phylogenetic tree. Additionally, since the number of combinations of sites can be enumerated by a binomial coefficient, there will obviously be many more combinations for intermediate numbers, relative to the extremes.

Phylogenetic diversity and variability

In certain cases, maintaining biodiversity requires proper allocation of funds, without which sites would eventually disappear. In other situations, the expansion of human activities requires the destruction of portions of habitats for the harvest of certain resources or the establishment of particular human structures such as buildings or farms. Both of these situations require expert knowledge of what is "expendable" and what is not, confronting us with "the agony of choice" (Vane-Wright et al. 1991). Ultimately, this means that reporting a certain ranking of sites or stating that a specific site contains the most diversity ensures that if there are only enough funds for the preservation of a single site, it will be preserved and others will not. The same problem would be encountered if the question was reversed and the site with the lowest PD rank had to be destroyed. Preservation problems that consider more than a single site require consideration of site combinations of sites, as discussed earlier. Consequently, the ranking of ecological communities on the basis of any criterion can be a risky operation and the variability associated with our estimates should be estimated and considered. This notion should be especially important in the case of phylogenetic diversity, as trees are probabilistically inferred on the basis of an evolutionary model rather than reported with absolute certainty.

Ever since phylogenies have been inferred using the maximum likelihood approach, attention has been given to the variance of the obtained estimates of branch lengths and their impact on the possibility of alternative topologies to the maximum likelihood estimate (Felsenstein 1981). Likewise, while Bayesian inference of phylogeny approaches the inference problem differently, it still addresses the issue of confidence in a tree (Holder and Lewis 2003). Therefore, it seems somewhat dangerous to base our conservation prioritization on a single evolutionary tree without any appraisal of its variability. As such, uncertainty about the tree should translate into uncertainty about the indices derived from it, such as PD. The use of any phylogeny without consideration for the variability of our estimates would represent an overestimation of the level of confidence placed in it. It could be argued that in cases where two or more competing tree topologies are to be considered, without a sound statistical reasoning to favour a particular one (e.g. Hasegawa and Kishino 1989, Kishino and Hasegawa 1989, Goldman et al. 2000), all these topologies would need to be considered. However, in our case, we are not interested in how particular topologies affect our estimates of phylogenetic diversity, but rather by how confident we can be in our assessment of phylogenetic diversity and the ranking of sites that ensues.

In the case of Cladocera, for which the relationship between species remains difficult to determine, placing absolute confidence in a single tree (topology with branch lengths) would be a dangerous procedure. Doing so would be at odds with the taxonomy, classification and phylogeny of the group, all of which have gone through considerable changes (Fryer 1987, Korovchinsky 1997) and are continually changing as the result of new discoveries, making the actual number and phylogenetic affinities of species of Cladocera difficult to know with certainty. This uncertainty is also due to the practical need for accurate species'

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identification outside of centers of taxonomic expertise, taxonomic reevaluation as well as the clarification of cryptic diversity in some species (Korovchinsky 1996, Forró et al. 2008). As such, knowledge about the status of the taxon as a whole is still growing, with recent discoveries of entirely new families such as Dumontiidae (Santos-Flores and Dodson 2003, Van Damme and Dumont 2008) and Nototrichidae (Van Damme et al. 2007), but also revisions of already established ones (e.g. Taylor et al. 2002, Bekker et al. 2012). Our estimates of phylogenetic relationships among cladoceran taxa based on mitochondrial DNA are not unequivocal, as even though the monophyly of Cladocera was supported and several originally-reported taxa were recovered, support for each of these is very variable and can be quite low.

Site PD comparison

Despite being most often considered in ecological diversity studies, the issue of PD estimation is intricately linked with phylogenetic inference. As such, special care should be given to the all facets of phylogenetic inference that can influence the results, such as substitution model and partitioning scheme selection. Our results emphasize the fact that phylogenetic data can bring information regarding both the PD values themselves, but also the uncertainty around them. The posterior distribution of Bayesian inference can give us an idea of the support we should lend to our obtained PD values. Often, the intervals for PD obtained spanned a wide range of values, reflecting the uncertainty in phylogenetic tree reconstruction. Likewise, comparison between sites' PD values and their ranking showed that phylogenetic data can bring support, or lack thereof, for prioritization choices. The framework considered for the comparison of a pair of sites can be extended to compare pairs of groups of sites by pooling sites' communities together. When considering sites PD ranks and the uncertainty

around them, it can be seen that several site comparisons should not be given any support when phylogenetic uncertainty is taken into account.

Additional considerations

Throughout this study, the question of whether or not consideration of the variability in the phylogenetic inference problem would affect the estimate of PD for a site and how this would affect reserve preservation prioritization choices was investigated. We have shown that the variability in phylogenetic estimates does affect PD and that such variation must be accounted for if it to be taken as a tool to help guide conservation issues. This component constitutes the first part of the species-specific sum of Weitzman's (1998) NAP. The second, more anthropocentric, part could also have been considered. Indeed, the ecosystem services of Cladocera, especially large filter-feeding cladocerans, are well known and their key role in aquatic ecosystems can affect algal biomass and nutrient loads (Shapiro et al. 1975, Peretyatko et al. 2009, Teissier et al. 2011). Additionally, they may also play a role in water safety issues, especially in urban environments, by impacting waterborne pathogens (Connelly 2007). Such utilitarian aspects could easily be incorporated into the NAP framework by adding this value to the pendant edge for the considered species (Hartmann and Steel 2006). However, PD has a straightforward meaning as the expected accumulated evolutionary history for the considered subset. When evolutionary history is measured in terms of branch lengths on an inferred gene-tree, as done here, the units are easily understandable, as the expected number of substitutions per site for sequences that evolve according to a time-continuous Markov process. However, if a utilitarian aspect is incorporated into PD, it may become a composite index whose individual components are hard to properly evaluate and compare. Indeed, it may prove difficult to assess or articulate on the same scale, the worth of cladoceran species' evolutionary heritage, relative

to their serviceable use as efficient grazers of phytoplankton or as bioindicators of safe waters. Such a debate is not the main focus of this paper, but it is nonetheless one that will eventually have to be resolved.

Other phylogenetic issues bound to affect PD values and conservation choices should also be taken into account. The source from which the phylogenetic material came should also be considered. In our case, organellar (mitochondrial) phylogenetic data was considered. However, nuclear phylogenies may give different results that can contradict those from mitochondrial DNA (e.g. Buckley et al. 2002). They may emphasize different conservation priorities by either suggesting different topologies, or by showing different branch lengths. We have chosen mitochondrial material as our basis upon which to establish site prioritization choices, but there seems to be no objective justification for this choice. We further note that the distinction need not be between organelles and the nucleus, as the same distinction can be made between other partitions of DNA datasets, such as genes alone. This raises another point that is also a current issue in phylogenetic reconstruction, which is the exact nature of what is being inferred. The distinction between "gene-trees" and "species-trees" is well established in the field of phylogenetics (Pamilo and Nei 1988, Maddison 1997, Nichols 2001, Edwards 2009). Consequently, we should also be aware that even if the tree were to be reconstructed with perfect accuracy (i.e. complete confidence in topology and branch lengths), it would still remain a gene-tree that shows the relationships between genetic lineages rather than a species-tree showing the relationship of the species that contain them. Discordances between the two are to be expected when the time between speciation events are short relative to the species' population sizes (Degnan and Rosenberg 2006 and 2009), making it such that they could theoretically happen anywhere on the tree. Even though the notion of PD can still be

reformulated with respect to the gene-tree, confusing the two could lead to misleading results regarding the affinities between the studied species.

The individual waterbodies were considered as conservation units, with their own distinct set of species. This view considers the waterbodies as static aquatic elements which do not communicate with each other, being scattered in an inhospitable terrestrial landscape. However, even though individual ponds are more or less clearly delineated, they may have connections with neighboring ponds and communities between waterbodies can interact with each other. Pond conservation policies should therefore also pay attention the ecology of the considered taxa, as well as to the possibility of networks of ponds in addition to isolated ponds (Boothby 1997, 1999 and 2000, Gibbs 2000, Jeffries 2005, E.P.C.N. 2007). This could mean that extremely close waterbodies, such as those in the botanical gardens (JBAlgues and JBNenuphars) could be considered as a single conservation unit due to their proximity which could allow population exchanges. Likewise, some of the populations in the ponds we sampled could be linked to those of other ponds which were not sampled, which would bring the need to consider these as well in conservation issues. Indeed, zooplankton dispersal between waterbodies is possible over a variety of scales (Cohen and Shurin 2003, Havel and Shurin 2004). However, even if dispersal to new waterbodies is possible, the local community diversity can affect colonization success by introduced species (Shurin 2000). Furthermore, increasing pressure due to the necessity of land for urban space and agricultural intensification have led to a considerable decline in the number ponds in some areas (Wood et al. 2003, Hassall 2014). Therefore, in some settings, such as urban environments, the number of aquatic habitats has been reduced, leading to a fragmented landscape which may limit zooplankton

dispersal. Consequently, the question of zooplankton dispersal, as well as the scale, extent and vectors of this process should be further assessed and evaluated in urban environments.

We used the Bayesian method for phylogenetic reconstruction as the posterior distribution of trees is directly the value of interest and has a clear interpretation. Furthermore, Bayesian analyses provide a method that simultaneously estimates trees and obtains measurements of uncertainty (Holder and Lewis 2003). However, the same analysis could also have been carried out using maximum-likelihood inference of phylogenies (Felsenstein 1981). In this case, the phylogenetic bootstrap (Felsenstein 1985) could have been used to generate a collection of trees from which confidence intervals for PD could be obtained. These intervals could be conventional bootstrap intervals (Efron 1979) or maybe bias-corrected and accelerated intervals (Efron 1981 and 1987), that have improved coverage probabilities and are second-order correct (Efron and Tibshirani 1993, Efron et al. 1996). The estimation of these intervals would be possible, but the generation of bootstrapped trees could be quite time demanding. Recent extremely fast algorithms for maximum-likelihood tree estimation and bootstrapping could help reduce this waiting time (Stamatakis et al. 2008, Stamatakis 2014).

Preserving phylogenetic diversity requires a thorough consideration of both species' presence/absence patterns, but also the variability of the genetic material and the probabilistic aspect of inferring phylogenies. The incorporation of phylogenetic information into biodiversity studies represents a worthwhile task that is sure to develop in near future. However, for it to become a well-founded basis upon which conservation prioritization choices are made, its relationship to the statistical aspects of model-based phylogenetic inference requires further elaboration. We have shown, with the use of Bayesian inference, that an appreciation of the variability around estimates is a critical step. Further developments

of these methods could be developed to carry out multiple comparisons between groups of sites or comparisons using different trees. Indeed, we could have used models with unlinked branch lengths or used approaches that make more direct use of the subset-specific rates, as they will eventually influence the expected amount of substitutions by multiplying the tree length by a constant. Increased collaborations between phylogeneticists and ecologists would increase the applicability of such methods.

3.6 Acknowledgments

Chapter 4

Spatio-temporal variation of community composition and feeding groups of zooplankton in urban waterbodies of a North American city

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4.1 Abstract

Waterbodies located in urban environments can serve more than just socio-economic functions, as they are ecologically interesting ecosystems that can contain noticeable amounts of urban biodiversity. Even though urban waterbodies have been the focus of various studies, the ecology of zooplankton communities, important ecological components of freshwater ecosystems, remains largely unknown. The communities of three of the main zooplankton taxonomic groups (cladocerans, copepods and rotifers) were followed in order to describe and explain zooplankton biodiversity patterns in these aquatic ecosystems. Community composition patterns differed between waterbodies, months and sampling zones, with significant interactions, indicating the necessity to consider all these factors. Communities comprised mostly of microphagous rotifers, raptorial rotifers and seston-feeding cladocerans. However, urbanization did not seem to select for a single type of feeding group composition pattern, as communities in waterbodies could shift between assemblages with different feeding types. Environmental variables, especially waterbody macrophyte coverage, were important factors for zooplankton biodiversity, positively affected species richness of various taxonomic groups and feeding groups. These variables also affected community composition, but they explained less variation, being modest predictor variables, indicating the need to consider other processes.

Keywords: Urban waterbodies, zooplankton communities, biodiversity, species richness, feeding groups, conservation management

4.2 Introduction

Small and generally shallow waterbodies, such as ponds, are common aquatic ecosystems found in all types of rural, urban and natural landscapes. For centuries, humans have been using ponds for a variety of services (e.g. source of food and water, industrial and aesthetic purposes), giving ponds an amenity value. Furthermore, such waterbodies have long attracted and fascinated humans, and have thus been integrated into their culture and history. These social and cultural values should be taken into account when assessing the value of pond ecosystems (Rees 1997, E.P.C.N. 2007, 2008, Boix et al. 2010).

Recent estimates showed that small lakes and ponds are extremely abundant at global scale (Downing et al. 2006), with their abundance being reevaluated through theoretical (Seekell and Pace 2011) and empirical studies (McDonald et al. 2012). Though often overlooked, small lakes and ponds are now seen as valuable ecosystems that play important roles in water balance, sedimentation and carbon cycle (Downing 2010). From a biological viewpoint, small waterbodies also represent non-negligible sources of biodiversity; they often contain several rare or unique species and can contribute notably to landscape diversity (Oertli et al. 2002, Wood et al. 2003, Williams et al. 2003). However, developing knowledge of pond and small lake ecology and biodiversity, as well as adequate conservation measures in perturbed habitats of rural and urban regions is still a work in progress. Ponds can be natural or artificial, and current interest in small waterbody conservation revolves not only with respect to how to best preserve those that already exist, but also how to create new ones as novel and ingenious ways to promote and preserve biodiversity (Williams et al. 1997, Davies et al. 2004, Williams et al. 2008, Garmendia and Pedrola-Monfort 2010). Recent efforts are being undertaken to study, promote and preserve their biodiversity in Europe (Biggs et al.

2005, Oertli et al. 2005a, Oertli et al. 2005b, E.P.C.N. 2007, 2008). However, in comparison, the assessment of the biodiversity and functioning of urban and rural waterbodies in North America is still in its beginnings.

The issue of biodiversity assessment and conservation policy elaboration may be especially important in the case of waterbodies located within urban environments. Urban ecosystems can be considerably different than more natural ones due to human presence and anthropogenic stressors (Alberti et al. 2003, Alberti 2005, Kowarik 2011). In urban environments, although waterbodies can be created by an array of natural processes, many are of artificial origin and may be constructed to fulfill various socio-economic "functions" or "needs". Indeed, urban waterbodies are used for a variety of reasons such as elements of recreational activities (fishing ponds, golf course, boating), parts of municipal parks and natural reserves, for managing pluvial and storm water, and for aesthetic purposes in urban landscape. The ecological value of urban waterbodies for biodiversity conservation thus may depend on the impacts of residential density, anthropogenic stressors, and human management. The presence of human populations and their associated activities have several and varied ecological effects on urban ecosystems and their associated biological communities. These effects can vary according to taxonomic groups (McKinney 2002, 2008, Alberti 2005). Some urban waterbodies are important sources of biodiversity, as they can provide refuges for several animal species and contribute to regional biodiversity (Hassall 2014). However, in some other urban waterbodies, aquatic macroinvertebrate and plant communities can exhibit poor ecological values (Noble and Hassall 2014). To develop management strategies to be able to monitor and preserve aquatic biodiversity in cities, it is essential to study the structure and biodiversity of aquatic communities in urban waterbodies.

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Zooplankton is an important component of aquatic food webs as it occupies a central trophic position, impacting both higher and lower trophic levels and consequently, the cycling of materials and energy (McQueen et al. 1986, Ghadouani et al. 2006, Finlay et al. 2007, Gélinas et al. 2007). Furthermore, zooplankton communities are highly responsive to various watershed perturbations (Pinel-Alloul et al. 1990, Patoine et al. 2000, 2002), including residential and land-cover disturbance (Gélinas and Pinel-Alloul 2008) and consequently, they are considered biological indicators of habitat quality (Jeppesen et al. 2011). Knowledge of zooplankton species distribution patterns in urban waterbodies, as well as of their ecology may also have practical uses such as for control of undesirable phytoplankton biomass, leading to cleaner and clearer waters (Peretyatko et al. 2009, Teissier et al. 2011), or as biological tools to assess water quality or contamination by waterborne parasites, as in lakes (Gannon and Stemberger 1978, Walseng et al. 2003, Nowosad et al. 2007). However, the biodiversity and ecology of zooplankton communities in urban environments remains largely undescribed and would require further knowledge in order to have a better idea of their conservation value and to be able to propose biodiversity conservation plans.

In this study, spatial and temporal patterns of zooplankton biodiversity were described in a set of nineteen urban waterbodies located on the city of Montreal in the province of Quebec (Canada), with zooplankton communities being followed monthly; from June to August of 2011. First of all, we wanted to assess whether or not established zooplankton community composition patterns in these waterbodies differ through time. A previous study of these waterbodies in the month of July 2010 (Mimouni et al. 2015) found an interaction between sampling zones and waterbody identity for various biodiversity metrics, wherein littoral vegetated zones were different than the open water zone and proved to be important

habitats for zooplankton biodiversity. However, as zooplankton communities can change over time, we asked: (i) is the interaction between site and zone for zooplankton community composition pattern consistent through time or not? In addition, urbanization can act as an ecological filter that will affect communities based on their ecological traits (Williams et al. 2009). Zooplankton taxa can differ markedly in biological traits, which constitute important aspect of their ecology (Barnett et al. 2007, Litchman et al. 2013) and on which urbanization can act on. Therefore, we asked: (ii) does urbanization lead to the development of a single type of zooplankton feeding group composition in urban waterbodies? To verify this, we classified the noted zooplankton taxa based on feeding ecology. Finally, the threatened nature of small urban waterbodies means that their communities are at risk. Therefore, we also asked: (iii) what are the main drivers of zooplankton richness and community composition patterns? We used a set of five environmental variables (total phosphorus concentration, surface area, mean depth, mean Secchi depth, and macrophyte cover), reported as being important for aquatic biodiversity (Jeppesen et al. 2000, Declerck et al. 2005) to see if these affected our communities and to be able to suggest biodiversity conservation methods.

4.3 Methods

4.3.1 Study sites and sampling design

Nineteen waterbodies of various types (including both permanent and temporary ponds, small lakes, as well as three wetlands), distributed over the Island of Montreal (Quebec, Canada) (45.46 - 45.69ºN, 73.50 - 73.90ºW), were sampled during the last two weeks in each

of the months of June, July and August of 2011 to survey zooplankton communities through

space and time (Figure 4.1).
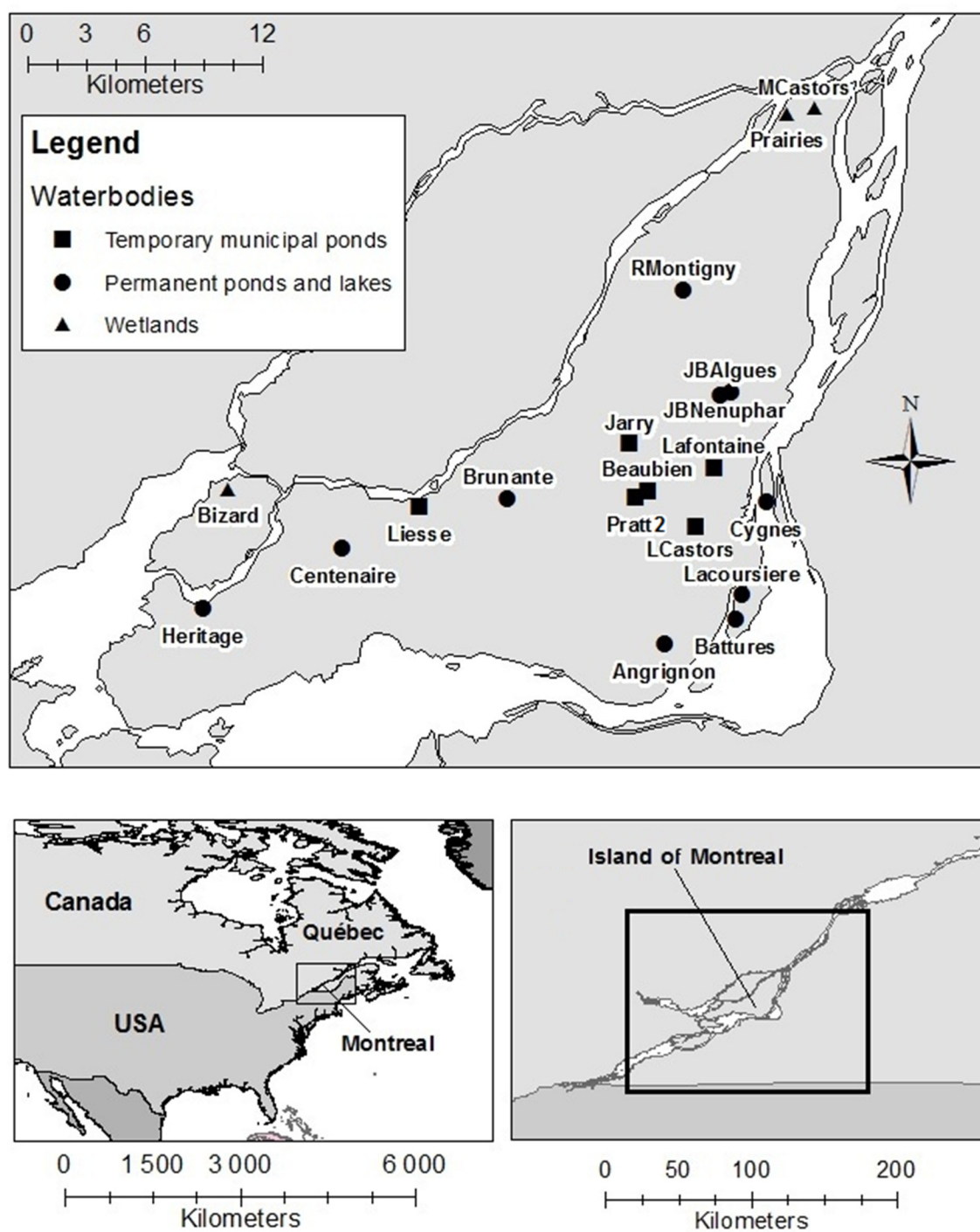
Figure 4.1: Geographic location and distribution of the 19 waterbodies sampled during the summer of 2011 on the Island of Montreal (Quebec, Canada). Modified from Mimouni *et al.*, 2015.

At each waterbody, depth and water transparency were measured using a Secchi disk at three pelagic sampling points; the results were averaged to obtain a single waterbody estimate. The sampled waterbodies are regularly surveyed by the City of Montreal water-quality monitoring program (Réseau de Suivi du Milieu Aquatique: http://ville.montreal.qc.ca). The program collects water samples from various waterbodies and carries out water chemistry analyses, including estimates of total phosphorus concentrations (TP). For the study, TP values as close as possible to the sampling dates for the zooplankton communities were selected and averaged into a summer value.

Within each waterbody, zooplankton communities in the pelagic (i.e. the center) and the littoral (i.e. the edge) habitats were sampled separately by randomly choosing three sampling points in the littoral zone, along with three pelagic points in the open-water area directly in front of these. This sampling scheme resulted in a total of six sampling units per waterbody. Zooplankton was sampled at each location from a small anchored inflatable boat using a 3 L bucket that was dipped ten times to arm's length in surface waters. The 30 L volume of water was subsequently filtered through a 54 μm mesh size plankton net. Organisms were narcotized with carbonated water and fixed with approximately 5 mL of pure formaldehyde in the field.

4.3.2 Taxonomic analyses

Zooplankton were kept in formaldehyde for approximately six months to fix the organisms and then transferred to a 75% ethanol and 5% glycerol solution to avoid desiccation, being concentrated into 25 mL scintillation vials. Except for when organic matter and detritus were too abundant or when densities were too high, a quarter of each well-mixed zooplankton sampling unit was taken using a pipette with a large-mouthed tip and transferred

to a Ward counting wheel (Ward 1955). Taxa were sorted and counted under a Leica Wild M3B stereomicroscope and identified with a Wild Heerbrug microscope to the finest possible taxonomic resolution (species and genus) using taxonomic keys for Rotifera (Edmondson 1959, Stemberger 1979, Nogrady et al. 1995, Haney et al. 2010), Cladocera (Brooks 1959, Hebert 1995, Haney et al. 2010), and Copepoda (Smith and Fernando 1978, Hudson and Lesko 2003).

4.3.3 Zooplankton feeding groups

Zooplankton species were classified into feeding groups based on their feeding ecology. Cladoceran feeding groups were established based on foraging mode, as in Declerck et al. (2007) and Barnett et al. (2007). Taxa that feed on periphyton or detritus on substrates or macrophytes were considered as substrate-grazing cladocerans. Taxa that actively filter the water column for phytoplankton or particulate organic matter were considered as seston-filtering cladocerans. The cladoceran taxa *Polyphemus pediculus* and *Leptodora kindtii*, which are predatory and obtain their food items differently than other cladoceran taxa (Young and Taylor 1988, Browman et al. 1989) comprised a separate feeding group of carnivorous cladocerans. Copepods were separated into raptorial cyclopoids and stationary and suspension-feeding calanoids (Barnett et al. 2007). Rotifer feeding groups were established on feeding strategies, as in Obertegger et al. (2011). We distinguished between microphagous taxa, which simultaneously collect food items, and raptorial taxa, which show an active grasping, piercing or pumping action to catch food items.

4.3.4 Analyses of variance

In order to try and answer the first two questions we had, three-way MANOVAs were used. With respect to the first question, to detect differences in species assemblages, zooplankton sampling units were differentiated using the square root of the Jaccard dissimilarity (Jaccard 1908) to take into account differences in community composition. The square root of the Jaccard dissimilarity was used as it is a Euclidean metric and will therefore produce no negative eigenvalues (Gower and Legendre 1986), but also because beta diversity based on it is related to other methods of calculation of beta diversity (Legendre and De Cáceres 2013). With respect to the second question, the abundances of each feeding group for each sampling unit were used following a Hellinger transformation (Legendre and Gallagher 2001). Because one of the sampling units of Battures was lost during sorting, this waterbody was not considered in these analyses.

The considered factors "Site" (waterbody identity), "Zone" (pelagic or littoral) and "Month" (June, July or August), as well as their possible two-way and three-way interactions were considered and coded as factors. Multivariate homogeneity of group dispersions was verified using the method outlined in Anderson (2006), as implemented in the *betadisper* function of the R package *vegan*, which was not significant (p-perm > 0.05 in both cases). The MANOVAs were carried out using the R function *adonis* of the R package *vegan*.

Following the detection of a significant three-way interaction, these were interpreted by creating interaction maps, as in Mimouni et al. (2015). In these cases, numbers were attributed to sampling units from all three months according to their groups determined by a k-means clustering. For the Jaccard dissimilarity, a principal coordinate analysis (Gower 1966) of the square-rooted distances was carried out beforehand. All obtained axes were retained and

used in the k-means analysis. For the Hellinger-transformed feeding groups data, the Caliński-Harabasz criterion (1974) showed a clear maximum at k = 3, which is the number of groups that was considered. However, for the community composition data, the criterion showed no clear maximum beyond k = 2. In this case, the SSI criterion was also considered (Borcard et al. 2011), which showed a local maxima at k = 10. After this value, other slightly higher values for the index were found, but these partitions were not considered, as a smaller number of groups would facilitate interpretation. We also note that this value is close to that which would have been obtained using Sturge's rule (9.28). The attribution of sampling units to groups showed how changes occurred between sites, months and zones. For the first question, LCBD indices for each sampling unit were computed and tested using the *beta.div* function of Legendre and De Cáceres (2013).

To further the interpretation of the obtained groups, distance biplots were drawn by carrying out ordinations of the zooplankton communities based on the selected metric (Jaccard dissimilarity or Hellinger distance) constrained on the groups obtained by k-means analysis. These ordinations were done using the *capscale* function of the R package *vegan*.

4.3.5 Zooplankton-environment relationships

In order to answer our third question and determine the main drivers of zooplankton species richness and community composition patterns, these were related to measured environmental variables. Environmental variables were individually transformed to reduce skewness. Waterbody mean depth (m) and surface (m^2), Secchi depth (m), and total phosphorus concentrations ($\mu g.L^{-1}$) were $\log_e$-transformed and macrophyte cover (%) was square-root transformed. To reduce the effects of temporal variation and habitat (pelagic/littoral) differences, which differed and would have affected species and feeding

group richness and community composition patterns, all species observed in each waterbody, based on all sampling units taken during the study, were considered.

To study zooplankton richness patterns, multiple regressions between the species richness of the various zooplankton taxonomic assemblages and feeding groups and the environmental variables were performed. These results were also compared with those of additional multiple regressions using the forward selection procedure of Blanchet et al. (2008). In order to make regression coefficients insensitive to variable measurement scales and be able to interpret them as explanatory weights, standardized regression coefficients are reported.

To study community composition patterns, redundancy analysis between the species presence-absence data and the environmental variables was carried-out. Before the analysis, the presence-absence matrix was Hellinger transformed (Legendre and Legendre 2012). In this case, the forward selection procedure of Blanchet et al. (2008) was also used, in order to remove any unimportant variable and to obtain a more parcimonious model. The proportion of variation explained for each taxa was computed using the *rdaTest* function of the R package *rdaTest*. Only taxa that had enough of their variation explained and represented in the biplot were drawn. Furthermore, using the variables retained by forward selection, variation partitioning (Borcard et al. 1992, Borcard and Legendre 1994, Peres-Neto et al. 2006) was considered, in order to compare the relative importance of these variables.

All statistical analyses were carried out in R 2.15.2 (R Development Core Team 2012) using the packages: *MASS* (Venables and Ripley 2002), *ape* (Paradis et al. 2004), *ade4* (Dray and Dufour 2007), *rdaTest* (Legendre and Durand 2010), *vegan* (Oksanen et al. 2012) and *packfor* (Dray et al. 2013)

4.4 Results

4.4.1 Waterbody environmental characteristics

The sampled waterbodies covered a broad range of morphometric and environmental characteristics (Table 4.1). Surface area was very variable and ranged from small ponds of a few hundred square meters to larger waterbodies that could be considered small lakes. Waterbodies were quite shallow and, except for one that had a deep pelagic zone (average depth > 9 m), most waterbodies were less than 2 m deep. Secchi depth was variable, and in some shallow ponds, light reached the sediment even in the open water zone. The waterbodies covered a range of phosphorus concentrations from oligotrophic values of 9.50 $\mu g.L^{-1}$ to hypereutrophic values of 265.33 $\mu g.L^{-1}$.

Table 4.1: General characteristics of environmental and morphometric variables for the 19 urban waterbodies sampled.

	Mean	Standard deviation	Minimum	Median	Maximum
Surface (m²)	27 592.43	34 331.73	392.12	11 395.41	114 466.60
Depth (m)	1.91	2.00	0.22	1.36	9.43
Secchi depth (m)	1.11	0.90	0.22	0.96	4.30
Total phosphorus (µg.L^{-1})	64.40	68.75	9.50	34.67	265.33
Macrophyte cover (%)	44.47	37.38	0.00	40.00	100.00

The waterbodies also differed in terms of macrophyte coverage, ranging from bare concrete ponds with no macrophytes to wetlands almost completely covered with dense macrophyte mats. Based on observations in 2011 and a visual campaign of the vegetation cover and dominance in 2012, fourteen waterbodies had aquatic vegetation in the littoral zone composed mainly of emergent (*Phragmites*, *Typha*, *Scirpus*, *Lythrum*, *Equisetum*, *Sparganium*, *Pontederia*, *Butomus*, *Alisma*), floating (*Nymphaea*, *Nymphoïdes, Lemna*, *Wolffia*) or submerged (*Potamogeton*, *Ceratophyllum, Anacharis* (*Elodea*), *Utricularia*, *Myriophyllum*, *Valisneria*, *Najas*) plants and some Characeae algae (*Nitella flexilis*, *Chara vulgaris*).

4.4.2 Zooplankton taxa and feeding group diversity

A total of 90 zooplankton taxa were recorded from the 19 waterbodies sampled over three months. The full taxonomic list of taxa is presented in Appendix A. Of these taxa, 60 were rotifers, 24 were cladocerans and 6 were copepods (3 cyclopoids and 3 calanoids). When results from all months were taken together, species richness of each waterbody was quite variable. The difference between the richest site (53 taxa) and the poorest site (12 taxa) was approximately four-fold, and sites contained on average 32 taxa (Table 4.2). Taxa also had quite heterogeneous occurrence patterns, with isolated incidences of certain taxa. Indeed, 12 taxa were present at only three sites, 12 others were present at only two sites and 12 other taxa were present at a single site (see Appendix 5 for the occurrences of each taxa). On the other hand, some taxa were observed at almost every site: *Keratella* sp. appeared in all 19 waterbodies; *Chydorus* sp., and *Lecane* (*Monostyla*) sp. in 18 waterbodies; Bosminidae and *Polyarthra* sp. in 17 waterbodies; and *Euchlanis* sp. in 16 waterbodies.

Table 4.2: Number of taxa of each assemblage (Rotifera, Cladocera, Copepoda), as well as the total number of zooplankton taxa, recorded in the 19 sampled waterbodies for each month (June, July, August) and the total summer survey.

	June				July			
	Rotifera	Cladocera	Copepoda	Zooplankton	Rotifera	Cladocera	Copepoda	Zooplankton
Pratt2	6	4	0	10	3	2	0	5
Beaubien	2	6	0	8	7	7	0	14
Heritage	16	8	3	27	16	9	0	25
Lafontaine	2	8	0	10	7	5	1	13
Centenaire	10	6	0	16	6	1	0	7
LCastors	15	12	3	29	17	4	3	24
Angrignon	13	11	1	24	16	9	1	26
Jarry	22	7	1	29	15	6	2	23
Cygnes	18	14	3	34	19	11	3	33
Brunante	20	8	1	29	15	8	4	26
Bizard	18	12	3	32	25	9	4	37
Liesse	6	7	0	13	2	7	0	9
Lacoursiere	24	9	3	36	22	10	3	34
Battures	8	7	1	16	4	4	0	8
JBNenuphars	18	13	4	34	19	12	4	34
JBAlgues	18	12	3	33	19	9	3	31
RMontigny	9	2	0	11	7	2	1	10
Prairies	10	6	2	18	16	6	3	25
MCastors	18	6	4	28	23	5	3	31

Table 4.2 (continued)

	August				Total			
	Rotifera	Cladocera	Copepoda	Zooplankton	Rotifera	Cladocera	Copepoda	Zooplankton
Pratt2	3	4	0	7	6	6	0	12
Beaubien	3	7	0	10	8	9	0	17
Heritage	7	2	1	10	22	10	4	36
Lafontaine	3	2	0	5	8	8	1	17
Centenaire	10	0	0	10	16	6	0	22
LCastors	14	3	1	18	26	12	4	41
Angrignon	13	4	0	17	20	12	2	33
Jarry	19	7	2	27	29	8	3	39
Cygnes	22	14	4	39	33	16	5	53
Brunante	8	5	2	14	21	9	4	33
Bizard	25	9	2	36	31	13	5	48
Liesse	2	6	1	9	6	8	1	15
Lacoursiere	26	8	3	36	35	12	5	51
Battures	4	7	1	12	9	8	2	19
JBNenuphars	27	11	3	40	31	14	4	48
JBAlgues	22	8	2	32	27	13	3	43
RMontigny	7	2	0	9	11	2	1	14
Prairies	16	6	2	24	21	7	3	31
MCastors	24	4	2	30	27	6	4	37

Most of the waterbodies showed a great deal of feeding diversity (Table 4.3). Indeed, out of the 7 possible feeding groups, 12 waterbodies had 6 represented and one waterbody had all 7 groups. Two waterbodies had 5 feeding groups, three had 5 and one had 3. Furthermore, in every waterbody, several taxa made up each feeding group. The feeding group composed of the largest number of representative taxa was the microphagous rotifers, followed by (in decreasing order), raptorial rotifers, substrate-grazing cladocerans, seston-filtering cladocerans, raptorial cyclopoids, stationary and suspension-feeding calanoids and carnivorous cladocerans.

Table 4.3: Zooplankton feeding groups recorded in the 19 sampled waterbodies, along with the number of taxa included in each feeding group (RRotifera: Raptorial Rotifera, MRotifera: Microphagous Rotifera, SGCladocera: Substrate-grazing Cladocera, SFCladocera: Seston-filtering Cladocera, CCladocera: Carnivorous Cladocera, RCopepoda: Raptorial Copepoda, SSF: Stationary and suspension-feeding Copepoda).

	RRotifera	MRotifera	SGCladocera	SFCladocera	CCladocera	RCopepoda	SSFCopepoda
Pratt2	1	5	4	2	0	0	0
Beaubien	0	8	5	4	0	0	0
Heritage	5	17	6	4	0	3	1
Lafontaine	2	6	1	5	2	0	1
Centenaire	4	12	3	3	0	0	0
LCastors	10	16	7	5	0	2	1
Angrignon	8	12	8	4	0	0	1
Jarry	8	21	5	3	0	1	1
Cygnes	9	24	10	5	1	3	1
Brunante	5	16	6	3	0	2	1
Bizard	12	19	9	4	0	3	1
Liesse	1	5	5	3	0	1	0
Lacoursiere	13	22	8	4	0	3	1
Battures	2	7	3	5	0	1	1
JBNenuphars	12	19	9	5	0	2	1
JBAlgues	12	15	9	4	0	2	1
RMontigny	4	7	0	2	0	1	0
Prairies	4	17	4	3	0	2	1
MCastors	9	18	4	2	0	3	1

Overall, rotifers and cladocerans were the predominant components of the zooplankton communities, while copepods only made up a small proportion of zooplankton communities (Figure 4.2). Amongst feeding groups, seston-filtering cladocerans, substrate-grazing cladocerans, microphagous rotifers and raptorial rotifers were the main components of the zooplankton communities. Some waterbodies, such as Beaubien and Prairies both had communities dominated by cladocerans in August, but these were seston-filtering cladocerans for the former and substrate-grazing cladocerans for the latter. Likewise, Lacoursiere and RMontigny both had communities dominated by rotifers in June, but these were microphagous rotifers for the former and raptorial rotifers for the latter. Furthermore, some sites showed proportional abundances dominated by the same feeding group in June, such as Lafontaine and LCastors, which both had communities more or less dominated by seston-filering cladocera, but diverging through time to end up with different communities in August: Lafontaine was dominated by microphagous rotifers and LCastors by raptorial rotifers.
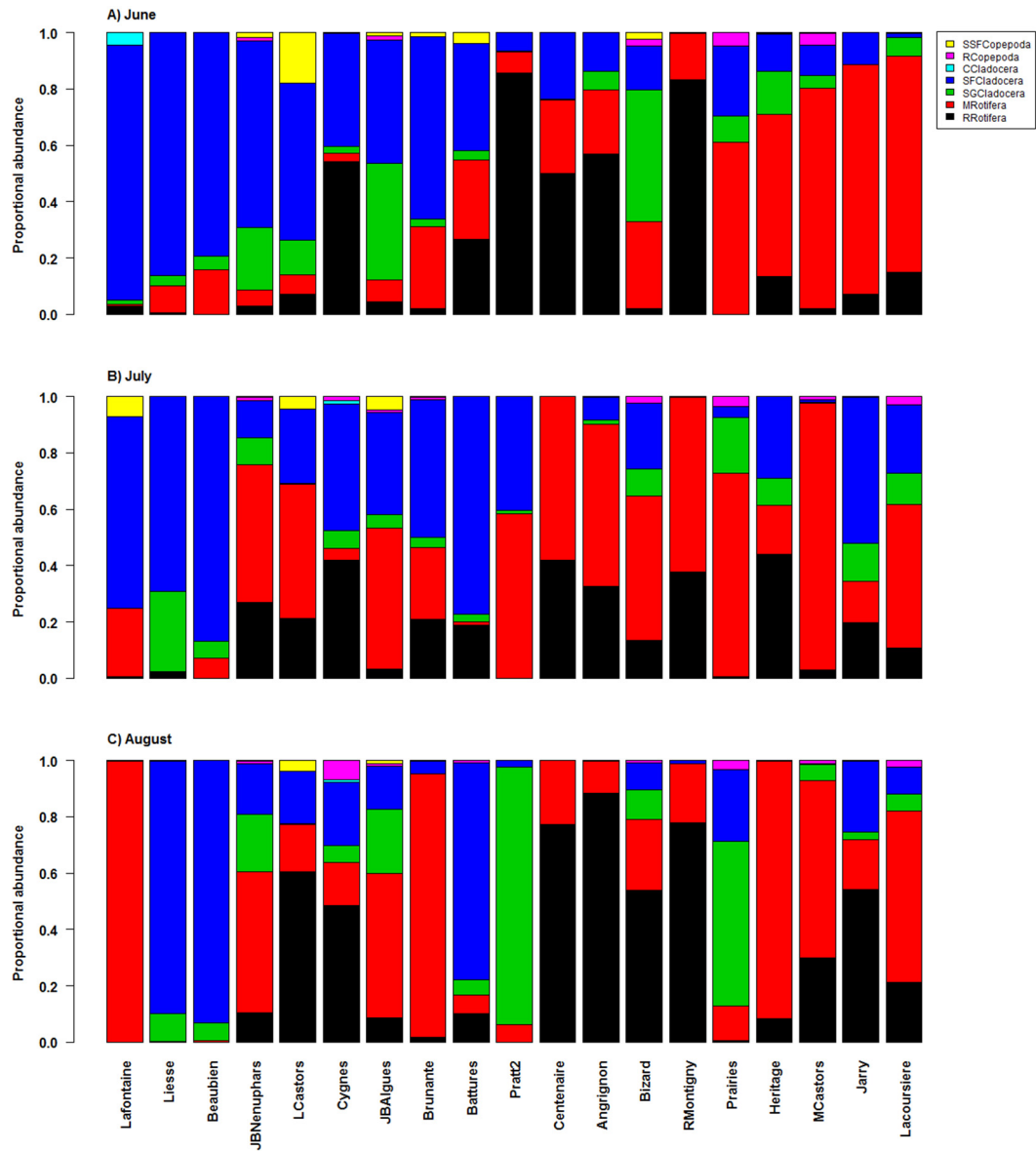
Figure 4.2: Barplots showing the proportional abundances of the zooplankton feeding groups (RRotifera: Raptorial Rotifera, MRotifera: Microphagous Rotifera, SGCladocera: Substrate-grazing Cladocera, SFCladocera: Seston-filtering Cladocera, CCladocera: Carnivorous Cladocera, RCopepoda: Raptorial Copepoda, SSF: Stationary and suspension-feeding Copepoda) for the months of June (A), July (B) and August (C) in the 19 sampled waterbodies.

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4.4.3 Consistency of community composition through time

A significant three-way interaction was found when performing the MANOVA using the square root of the Jaccard dissimilarities of zooplankton community composition between sites, months and zones (p-value < 0.05 after 9999 permutations). Owing to this significant interaction, the shape of the two-way interaction between the factors "Site" and "Zone" would differ between months and the results of each month should be considered separately.

The interaction map for community composition (Figure 4.3) showed that most of the differences were between waterbodies, with some differences between months and with differences between zones showing up in only a few cases. Indeed, several waterbodies (e.g. MCastors, Prairies, JBNenuphars and JBAlgues) tended to remain in the same group, differing only slightly over time. Other waterbodies, such as Bizard or Beaubien, showed different community compositions between months. Finally, in some cases, such as Cygnes in July, differences in community composition between zones within a waterbody were seen.
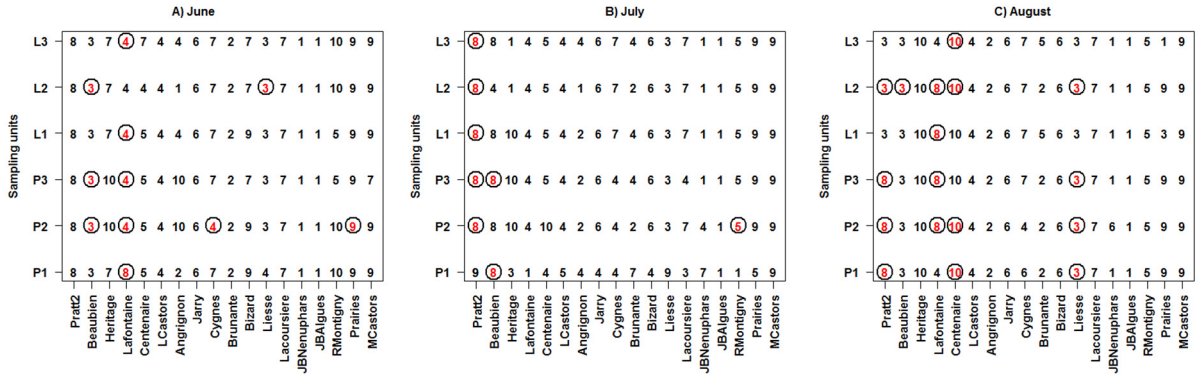
Figure 4.3: Interaction map showing the attribution of zooplankton taxonomic composition data to groups as determined by a k-means partitioning applied to the Jaccard dissimilarity principal axes for each month sampled (A: June, B: July and C: August). Numbers for each sampling unit correspond to the group to which it belongs. Site names are noted on the abscissa and sampling units (P1-P3 from pelagic zone and L1-L3 from littoral zone) on the ordinate. Sampling units with significant LCBD values are drawn in red with a circle around the number.

Significant interactions prevented us from analyzing the effects of each factor independently. However, based on the interaction maps, it appeared that, when compared to variation within the same waterbody between months or to variation between waterbodies through time, the differences between zones in a waterbody are less important. Nonetheless, the interaction does indicate that, even though they are less important or noticeable, differences between the two zones (littoral vs. pelagic) within waterbodies should be considered. Most of the significant LCBD values were associated with groups 8, 3 and to a lesser extent 4 and 10.

The constrained analyses of principal components showed differences in both group location and in group dispersal (Figure 4.5). On the first two dimensions, the polygons associated with each determined group were not very well delimited. The first axis mainly differed between groups that had a very diverse assemblage of zooplankton taxa (groups 9, 1, 6 and 7) and those that had communities with a more modest amount of taxa (groups 5, 2, 10 and 4). Along the second axis, the polygons for two groups distinguish themselves from the rest: those for groups 3 and 8. They were associated with communities made up mostly of cladoceran taxa (SCRA, SIMO, CERI). It should be noted that these are the groups within which most of the significant LCBD values are found.
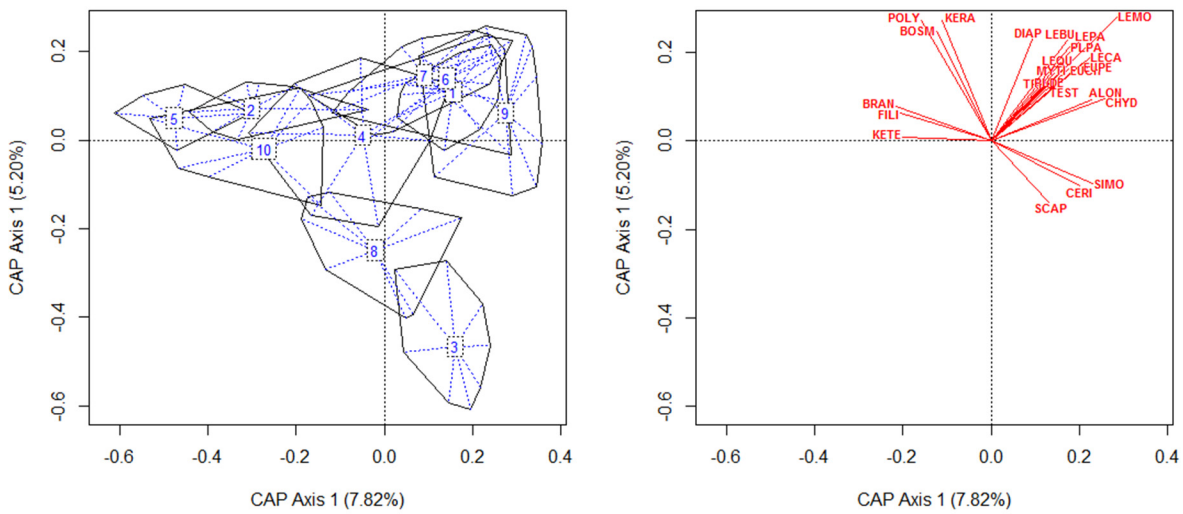
Figure 4.4: Distance biplot based on the CAP ordination of the zooplankton communities constrained by the groups, as determined by k-means clustering. In order to interpret only species that contribute to discriminating groups and to improve legibility, taxa with small loadings on the canonical axes were not drawn. See Appendix 5 for the names of the taxa.

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4.4.4 Effects of urbanization on zooplankton feeding groups

A significant three-way interaction was also found when performing the MANOVA using the Hellinger distance of zooplankton feeding groups between sites, months and zones (p-value < 0.05 after 9999 permutations). Owing to this significant interaction, we can establish that there is no single dominating zooplankton feeding groups in between sites, months and zones in urban waterbodies.

The interaction map for feeding groups (Figure 4.5) also showed that most of the differences were between waterbodies, with some differences between months and with differences between zones showing up in only a few cases. For some waterbodies, communities often changed noticeably between months, such as Lafontaine, which changed from group 1 in June to group 3 in August or LCastors, which went from group 1 in June to group 2 in August. For other waterbodies, such as MCastors, communities remained the same over the summer period. Differences between pelagic and littoral zones occurred for certain sites, such as Heritage in June and July, and Bizard in June.
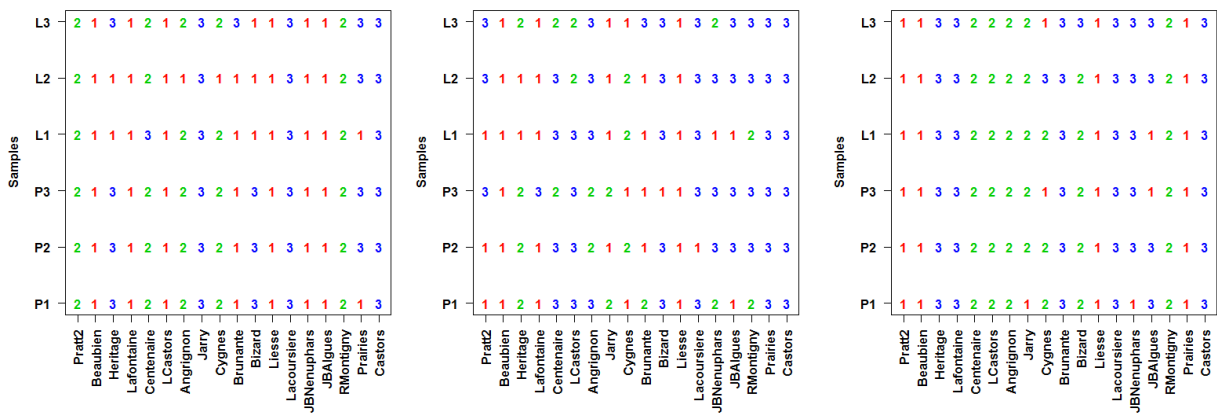
Figure 4.5: Interaction map showing the attribution of zooplankton sampling units to groups as determined by a k-means partitioning applied to the Hellinger-transformed feeding groups data for each month sampled (A: June, B: July and C: August). Numbers for each sampling unit correspond to the group to which it belongs. Site names are noted on the abscissa and sampling units (P1-P3 from pelagic zone and L1-L3 from littoral zone) on the ordinate.

The polygons for each group of sampling units were quite well defined in the case of species feeding group data (Figure 4.6). Indeed, the constrained redundancy analysis showed three well-defined groups, with each having one or two mainly defining feeding groups. The first axis mainly distinguished between groups that had sampling units which had a higher relative abundance of rotifers (groups 2 and 3) and group 1, which had a higher relative abundance of cladocerans. However, taking into account zooplankton species feeding groups revealed further differences along the second axis. In this case, group 3 had a higher relative abundance of microphagous rotifers, whereas group 2 had a higher relative abundance of raptorial rotifers. Group 1 had a higher abundance of seston-filtering cladocera, with some substrate grazing-cladocera.
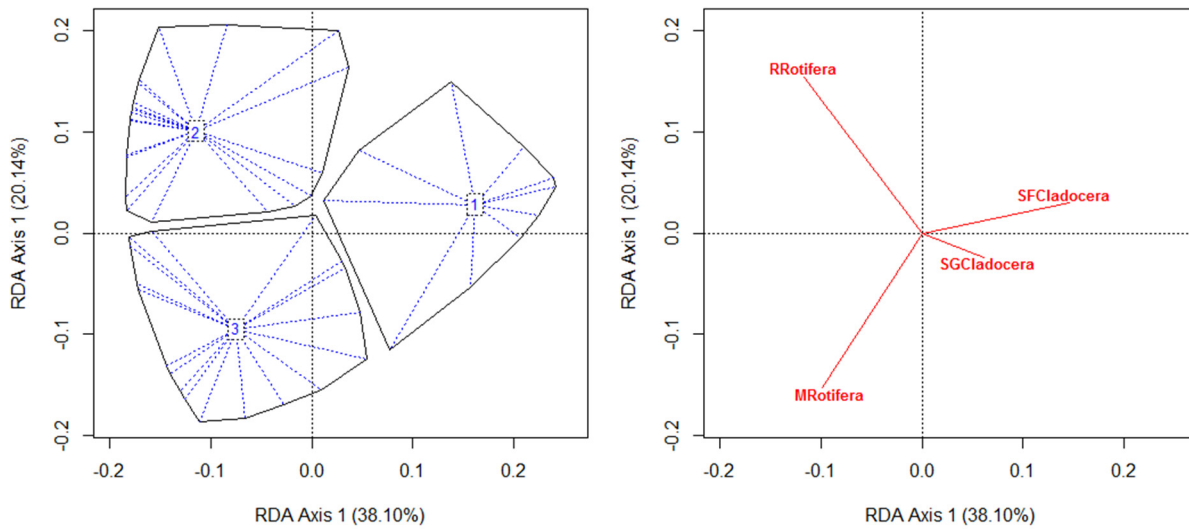
Figure 4.6: Distance biplot based on the CAP ordination of the zooplankton communities constrained by the groups, as determined by k-means clustering. In order to improve legibility, the vectors for the feeding groups CCladocera, RCopepoda and SSF, which had small loadings on the canonical axes, were not drawn.

4.4.5 Relationships between zooplankton biodiversity and environmental features

Significant relationships between zooplankton species richness and the environmental variables were observed. For almost all zooplankton taxonomic groups, macrophyte coverage and Secchi depth were the only variables retained (model p-value < 0.05 in all cases; Table 4.4). Forward selection of variables did not produce different results, instead most often adding Secchi depth as a significant explanatory variable. In all cases when they were significant, macrophyte coverage and Secchi depth had a positive impact on species richness. Furthermore, these variables usually showed much higher standardized regression coefficients than the other variables considered, especially macrophyte coverage. Only for cladocerans was macrophyte coverage not retained by forward selection. However, it should be noted that when waterbody mean depth is omitted, then both considering all variables and using forward selection lead to Secchi depth, macrophyte coverage and total phosphorus concentrations having significant effects on cladoceran species richness. In this case, cladoceran species richness decreased with increasing total phosphorus concentrations.

Table 4.4: Significant variables, standardized regression coefficients (b), and adjusted R^2 (R^2_{adj}) based on multiple regressions either using all the variables, or only variables retained after forward selection, for the different zooplankton taxonomic groups and feeding groups. Only significant models are reported. Area: surface (m^2), Depth: mean depth (m), Secchi: Secchi depth (m), TP: total phosphorus ($\mu g.L^{-1}$), Macr: macrophyte cover (%).

	Taxonomic assemblages					
	Zooplankton					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	0.10	-0.01	0.38	-0.16	0.66	0.68
Forward selection	Macrophytes, Secchi	-	-	0.46	-	0.64	0.70
	Rotifera					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	0.15	0.09	0.20	-0.15	0.70	0.60
Forward selection	Macrophytes, Secchi	-	-	0.37	-	0.65	0.62
	Cladocera					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes, Secchi	-0.07	-0.32	0.80	-0.25	0.35	0.65
Forward selection	Secchi, Depth	-	-0.70	1.21	-	-	0.60
	Copepoda					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	0.07	0.05	0.36	0.17	0.60	0.51
Forward selection	Macrophytes, Depth	-	0.38	-	-	0.70	0.57
	Feeding groups					
	Raptorial rotifers					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	0.27	-0.17	0.33	-0.16	0.66	0.64
Forward selection	Macrophytes, Secchi	-	-	0.34	-	0.66	0.60
	Microphagous rotifers					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	0.06	0.26	0.09	-0.14	0.66	0.44
Forward selection	Macrophytes, Depth	-	0.36	-	-	0.68	0.51
	Substrate-grazing cladocera					
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	-0.12	-0.15	0.52	-0.24	0.47	0.42
Forward selection	Macrophytes, Secchi	-	-	0.42	-	0.48	0.42

	Seston-filtering cladocera						
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Secchi	-0.01	-0.39	0.85	-0.25	0.29	0.62
Forward selection	Secchi, Depth	-	-0.11	0.56	-	-	0.59
	Carnivorous cladocera						
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	-	-	-	-	-	-	-
Forward selection	-	-	-	-	-	-	-
	Raptorial cyclopoids						
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macropyhtes	-0.02	0.17	0.23	0.20	0.56	0.34
Forward selection	Macrophytes	-	-	-	-	0.61	0.34
	Stationary and suspension-feeding calanoids						
	Significant variables	b_{Area}	b_{Depth}	b_{Secchi}	b_{Phos}	b_{Macr}	R^2_{adj}
All variables	Macrophytes	0.29	-0.26	0.59	0.04	0.53	0.60
Forward selection	Macrophytes, Secchi	-	-	0.47	-	0.57	0.62

Zooplankton feeding groups also responded to the measured environmental variables. As for taxonomic groups, macrophyte coverage and Secchi depth came out as important variables affecting feeding group diversity. For the case of carnivorous cladocerans, regression residuals were not normally distributed so a permutational test was considered, which ended up not being significant.

Zooplankton assemblages were affected by the measured environmental variables as the RDA model was significant (p-perm < 0.05 after 9999 permutations). Forward selection of variables using the forward selection procedure of Blanchet et al. (2008) retained the three variables "macrophyte coverage", "waterbody area" and "total phosphorus concentration". The RDA model relating zooplankton community composition and these three variables differentiated communities along two main axes (Figure 4.7). The first of these axes accounted for 14.66% of the variation in community composition and mainly differentiated communities along an axis of macrophyte coverage. Most of the species which were well-explained by the model were related to this gradient in macrophyte coverage, as up to 13 taxa showed positive correlations with the first axis, whereas only a 2 taxa showed negative correlations with it. The second axis accounted for 9.91% of the variation in community composition and differentiated communities along an axis of waterbody size and productivity. Fewer species were associated with this gradient, although a group of cladocerans (CERI, CHYD, ALON, SIMO) were more often associated with smaller and less productive waterbodies and a group of rotifers (ASBR, CONO, BRAN, FILI) were were more often associated with larger and more productive waterbodies.
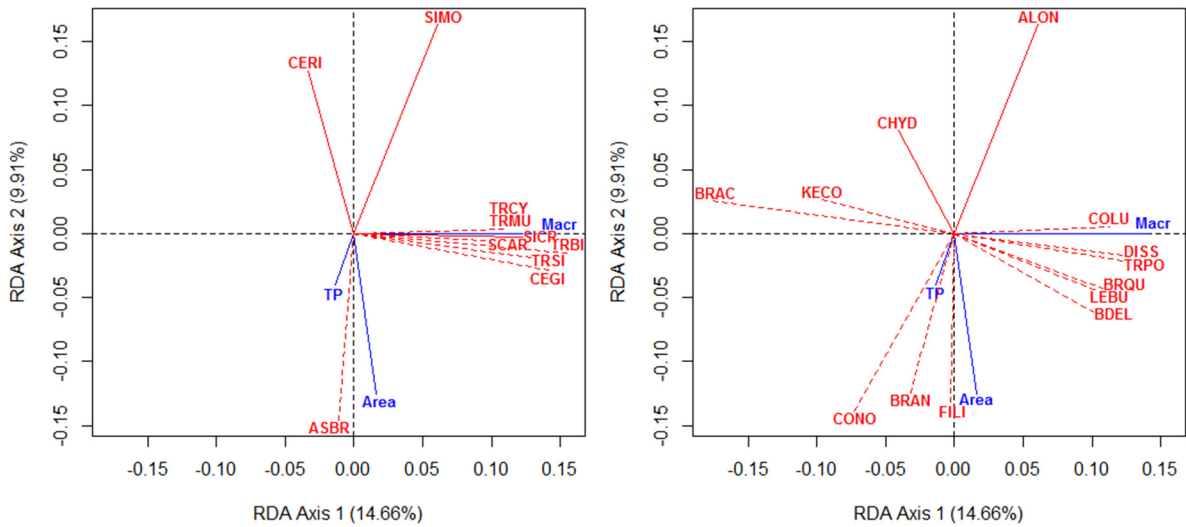
Figure 4.7: Ordination plots of the RDA model describing zooplankton communities and the environmental variables retained by forward selection. The first canonical axis accounted for 14.66% and the second axis for 9.91% of the variation in zooplankton community composition. The left panel shows the species vectors for raptorial rotifers and seston-filtering cladocerans, and the right panel shows the species vectors for microphagous rotifers and substrate-grazing cladocerans. In order to retain only important taxa and improve legibility, only taxa that were well explained by the analysis and well represented in the two-dimensional space are represented. See Appendix 5 for the names of the taxa.

Variation partitioning showed that an appreciable amount of the variation in zooplankton richness was due to macrophyte coverage which accounted for 39.60% of the variation, as well as by Secchi depth, which accounted for 19.74% (Figure 4.8A). Both of these fractions were significant (p-value < 0.05 after 9999 permutations). Likewise, most of the variation in zooplankton community composition was also explained by macrophyte coverage, followed by waterbody area then total phosphorus concentrations (Figure 4.8B). Indeed, 11.10% of the variation was accounted for by macrophyte coverage, 5.57% by waterbody area and 2.46% by total phosphorous. All three individual fractions were significant (p-value < 0.05 after 9999 permutations). There were practically no shared fractions of variations between variables, and only 0.17% of the variation was shared by all three variables.
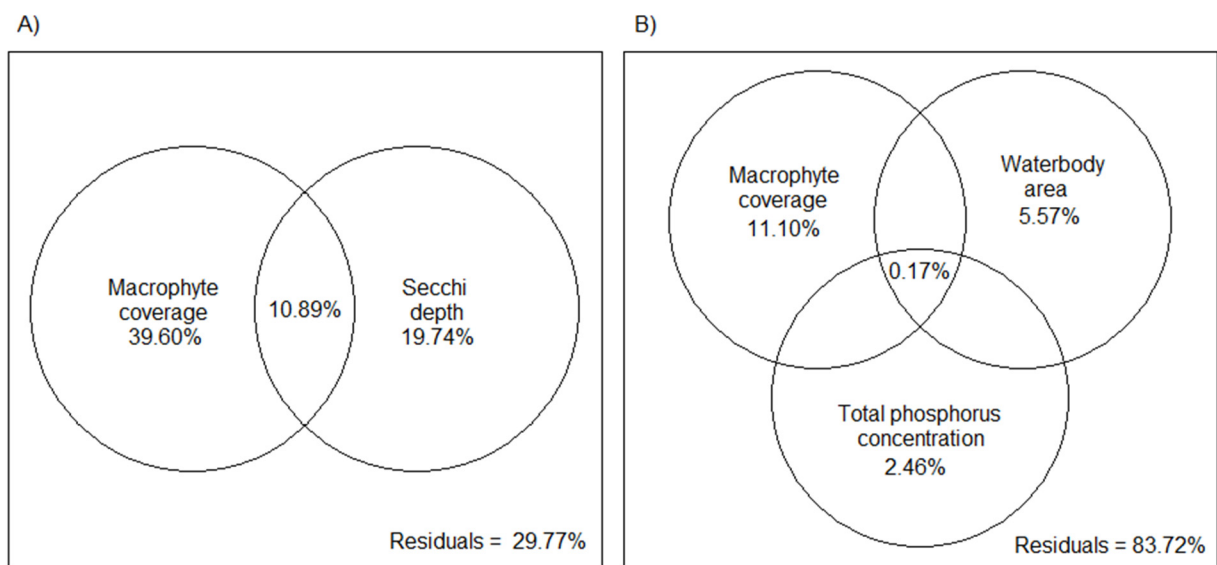
Figure 4.8: Venn diagram showings showing the partitioning of the variation in zooplankton species richness (A) and zooplankton community composition (B) between the environmental variables retained by forward selection. The values reported are adjusted coefficients of multiple determination.

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4.5 Discussion

Small waterbodies are a common feature in urban environments and they may play an important role in preserving biodiversity by acting as reservoirs of biodiversity. However, relative to other taxonomic groups (Hassall 2014), knowledge of zooplankton communities in urban waterbodies is still relatively unknown. Studies that have focussed on the biodiversity of zooplankton in urban waterbodies have shown that, despite the presence of human activities and stressors, urban waterbodies can contain noticeable amounts of zooplankton biodiversity and are not poor in biodiversity (Langley et al. 1995, Ejsmont-Karabin and Kuczyńska-Kippen 2001, Mimouni et al. 2015). Therefore, the biodiversity potential of urban ponds with reference to zooplankton communities should not be ignored. Based on a summer campaign, we found that urban waterbodies in Montreal were found to be relatively diverse, containing up to 90 zooplankton taxa, several of which had very restricted distributions, appearing in only a few waterbodies. The communities also showed a rather high amount of feeding ecology diversity, with a high number of zooplankton feeding types and with each feeding group being represented by several taxa with similar feeding strategies.

The littoral zone of waterbodies which is often more structurally complex and contains macrophytes, is recognized as an important contributor to biodiversity (Walseng et al. 2010, Vadeboncoeur et al. 2011, Mimouni et al. 2015). Mimouni et al. (2015) found littoral vegetated zones proved to be important habitats for zooplankton biodiversity, contributing considerably to the species richness pool, often with a different species composition. However, these were only based on a single campaign in July. Since zooplankton communities in temporary waterbodies (Mahoney et al. 1990, Sahuquillo and Miracle 2010) as well as in permanent lakes (Hairston Jr. et al. 2000) can change through time, there is reason to suspect

that the observed interaction between waterbody identity and sampling zone can be different depending on the considered month.

The significance of the three-way interaction between site identity, month and sampling zone in our MANOVA analysis supports this claim, as it indicates that none of the two-way interactions should be considered without the third factor. Particularly, the interaction between site identity and sampling zone is liable to change between months. Such changes are important to conservation evaluation, as they imply that estimates of zooplankton community composition in urban waterbodies can differ notably through time. Furthermore, the waterbodies that contained sampling units with significant LCBD changed between months, which would make the consideration of month necessary. Consequently, to fully monitor zooplankton communities and assess their biodiversity in urban environments, such temporal variability should be accounted for. The interaction maps showed that most of the differences were between waterbodies within months or within waterbodies between months. Indeed, the interaction maps also showed that the waterbodies which contained sampling units with significant LCBD values changed over time. Even though the significant three-way interaction implies that differences between the two zones (littoral vs. pelagic) should be considered, differences between zones in a waterbody were rarely seen at this level of grouping.

Seasonal changes in environmental factors of lakes can be important drivers of zooplankton community succession. Indeed, the well-known Plankton Ecology Group (PEG) model describes zooplankton succession as the result of a combination of both intrinsic and extrinsic factors (Sommer et al. 1986, Sommer et al. 2012). However, this model is unlikely to apply to small and shallow waterbodies such as ponds because ponds are quite ecologically

distinct from larger lakes (Oertli et al. 2002, Søndergaard et al. 2005, Scheffer et al. 2006, Meerhoff and Jeppesen 2009). Even so, small waterbodies should still show some level of seasonal and/or environmental predictability, to which zooplankton communities could respond, potentially determining their succession through time.

Zooplankton species can vary considerably regarding their ecological traits, whose analysis can reveal insights into ecosystem processes (Barnett et al. 2007, Litchman et al. 2013). Their feeding ecology is quite varied as individual species can differ in their prey items, but also in the way they obtain them. For certain zooplanktonic groups, such as rotifers, considering feeding group can constitute an informative term (Wallace and Snell 2010, Obertegger et al. 2011). Urban environments can be considerably different than more natural ones due to human presence and anthropogenic stressors, which affects ecosystem biodiversity and processes (Collins et al. 2000, Alberti et al. 2003, Alberti 2005, Kowarik 2011). Urbanization establishes a set of environmental filters that impact biological communities, favoring the development of some species and leading to the disappearance of others (Williams et al. 2009). Some of these changes in species abundance can be non-random and can be the result of the presence of a strong selector for species composition based on their ecological traits. Therefore, it could be that, in urban waterbodies, these urban filters affected zooplankton communities and led to the establishment of a single kind of zooplankton feeding group composition across all urban waterbodies.

However, despite their location in an urban environment and the presence of anthropic stressors, zooplankton communities in urban waterbodies showed important differences in term of the dominant feeding groups and this dominance could change between months and sites. Cluster analysis revealed that most sampling units were spread among three groups, for

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which taxa belonging to raptorial rotifers, microphagous rotifers and seston-filtering and substrate-grazing cladocera were the main components. The main axis of differentiation was between sampling units either dominated by cladocerans or rotifers. This inverse relationship between the abundances of cladocerans and rotiferans has been reported from other aquatic ecosystems (Adalsteinsson 1979, Gilbert 1988, Lampert and Rothhaupt 1991, Gervais et al. 1999). Such alternating patterns could be due to competitive interactions between these two taxonomic assemblages (Gilbert and Stemberger 1985, Gilbert and MacIsaac 1989, MacIsaac and Gilbert 1989, 1991a, 1991b). Furthermore, we note that an even further distinction can be made between raptorial rotifers and microphagous rotifers, which formed two well-defined clusters. Such differences in rotifer communities can also be associated to changes in cladocerans communities and in trophic state (Obertegger et al. 2011, Obertegger and Manca 2011, Spoljar 2013). Therefore, urban waterbodies would show seasonal alternances between zooplankton feeding groups, which would be the result of biotic interactions and possibly changes in trophic state, rather than environmental filtering selecting for the dominance of a single feeding group pattern.

Within each waterbody, the same feeding group could be represented by several taxa. We considered only between taxon variations, but the possibility that taxa may exploit other resources should also be considered. For example, *Daphnia* can feed on periphyton, as well as on phytoplankton (Siehoff et al. 2008). Furthermore, functional groups established solely on mean feeding traits neglects other important ecological aspects such as habitat preferences. For example, *Sida crystallina* and *Simocephalus* sp. are considered filter-feeders, but they can have strong associations with macrophytes in the littoral zone, rather than occurring in open-water zone. Furthermore, even for "free-swimming" cladocerans, the littoral zone can provide

a refuge from some predators for under certain conditions (Burks et al. 2001a, Burks et al. 2002). Likewise, an even greater level of community trait differentiation can be obtained when also considering the distances between setulae for filtering cladocerans (Geller and Müller 1981), which can affect the efficiency of retention as well as the type of food items selected. Finally, temporal partitioning of resources may also play a role in allowing several taxa to occupy the same feeding group or exploit similar resources, as all zooplankton taxa do not appear at the same time within waterbodies. Perhaps it is this further partitioning of ecological habitats, functional traits and niches that allow so many taxa to occupy the same feeding group.

Zooplankton species richness was affected by waterbody environmental features, with slightly different responses depending on which taxonomic or feeding group was considered. However, one variable that was almost consistently found across all groups was macrophyte cover. When it was retained, an increase in macrophyte cover was always related to an increase in species richness. This can be explained by the fact that macrophytes offer a structurally complex habitat, where some species may find ameliorated food conditions or refuge from certain predators (Burks et al. 2001a, Burks et al. 2002). In a study of shallow waterbodies across Europe, Declerck et al. (2005) also found that macrophyte cover was an important variable for the species richness of several aquatic organisms. For shallow lakes and ponds, macrophytes have been indicated as a key element in increasing invertebrate diversity (Scheffer et al. 2006). Secchi depth was also often noted to affect zooplankton species richness, which could suggest an effect of water clarity or turbidity in shaping zooplankton communities.

Studies have reported relationships between zooplankton species richness and morphometric variables such as depth (Keller and Conlon 1994) or waterbody surface area (Dodson 1992, Allen et al. 1999, Dodson et al. 2000). These relationships would be related to the fact that larger and deeper lakes are usually stratified and show a greater variety of possible habitats for zooplankton. However, in this study, surface area was never a significant variable for either taxonomic or feeding group species richness and mean depth only contributed significantly to species richness in some taxonomic (cladocera and copepoda) and feeding groups (microphagous rotifer and seston-filtering cladocera). This result could be due to the limited number of waterbodies considered and the fact that other studies (Dodson et al. 1992, Allen et al. 1999, Søndergaard et al. 2005) considered larger waterbodies. However, the absence of significant relationships between the species richness of the various zooplankton assemblages and the morphometric variables could be due to a stronger relationship between species richness and habitat diversity. Indeed, waterbodies with more macrophyte coverage would offer a higher diversity of habitats for zooplankton communities. If macrophyte communities are a key element in increasing invertebrate diversity in small waterbodies (Scheffer et al. 2006); then the absence of a relationship between waterbody size and macrophyte cover would explain why zooplankton species richness did not seem to increase with waterbody surface area.

Considering community composition data rather than simple richness values gave somewhat different results. Both analyses agree that macrophyte coverage is an important variable for maintaining rich and diverse zooplankton assemblages. Indeeed, in the RDA, macrophyte coverage accounted for most of the variation out of the three environmental variables and the first axis was essentially a gradient of macrophyte coverage. Several taxa,

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mostly raptorial rotifers and microphagous rotifers, but also the cladoceran *Sida crystallina* were positively associated with macrophyte coverage. In contrast, the microphagous rotifers *Keratella* sp. and *Brachionus* sp. were negatively associated with this gradient. Therefore, macrophytes still offer a varied habitat that increases the diversity of zooplankton communities. However, aside from this variable, the two analyses disagreed with respects to the remaining variables. Secchi depth was not an important variable for zooplankton community composition. Instead, the second axis was mostly an axis of waterbody size and productivity. Consequently, it could be that zooplankton species richness and community composition patterns are governed by some similar variables (such as macrophyte coverage), but that they differ for other variables.

Furthermore, it should be noted that, relative to the regressions of zooplankton richness, for which coefficients of multiple determination were quite high (between 0.34 and 0.70), that value for the redundancy analysis was considerably lower (0.16). Therefore, though the measured environmental variables proved to be very good predictors of taxonomic and feeding group species richness, they could be considered modest predictors of community composition patterns. Consequently, it is important to further elaborate on the role that macrophytes, among other environmental variables and processes, play in shaping zooplankton communities. In regression analyses, macrophyte coverage was almost always included in models and explained a sizeable portion of richness variation. Likewise, in the RDA, it also accounted for most of the variation in community composition. However, the lower value for community composition would indicate that it is less effective as to which taxa actually fill these spots. Small waterbodies can exhibit high regional diversity as the consequence of several mechanisms, including variation in specific local conditions and

variable hydroperiods or from stochastic events associated with dispersal limitation or priority effects (Scheffer et al. 2006). Therefore, solely increasing the macrophyte coverage and the water clarity should not be enough maintain zooplankton diversity and interest should also be given to other factors and processes.

The preservation of aquatic biodiversity in urban environments is a current and difficult issue. Based on our results, a few important environmental variables are important drivers of zooplankton richness in urban waterbodies, namely macrophyte cover and water transparency. However, these affect only part of zooplankton diversity, as they are not as good descriptors of community composition patterns. Therefore, other additional environmental factors or biological processes could affect zooplankton community composition in urban ponds. It has been suggested that conservation policies aimed at preserving regional diversity should consider all waterbody size ranges (Oertli et al. 2002), flow, size, and permanence regimes (De Bie et al. 2010), as well as early and late successional stages (Hassall et al. 2012) of ponds on the landscape. Consequently, the maintenance of a diversity of waterbody types at regional scales should also be considered for aquatic biodiversity preservation. Future studies should seek to elucidate how zooplankton communities in urban waterbodies form as well as evaluate how much of community composition is due to environmental control and biotic interactions, such as competition, as well as the scales at which these processes occurr.

4.6 Acknowledgements

Chapter 5

Conclusion

5.1 General discussion

The management of freshwater ecosystems and their resources constitutes an important challenge for mankind, which depends on them for several reasons. In addition to sources of water for drinking or sanitary purposes, freshwater ecosystems are also, among others, sources of irrigation water for agriculture, goods such as food and materials, hydroelectric power generation, as well as of recreation opportunities (Postel and Carpenter 1997, Wilson and Carpenter 1999). In addition to these services, freshwater ecosystems are also important sources of biodiversity, as they contain around 9.5% of the total number of animal species recognized globally (Balian et al. 2008). Amongst these ecosystems, ponds and small waterbodies have emerged as important ecosystems that can contain noticeable amounts of biodiversity. Indeed, ponds have been noted to contain several species noted as rare or unique and can contribute noticeably to landscape diversity (Oertli et al. 2002, Williams et al. 2003, Wood et al. 2003). However, they remain at risk from a number of threats, such as increased pollution in organic contaminants and heavy metals, changes in their trophic state and pH, habitat loss due to changes in land use, invasive species and global change (Brönmark and Hansson 2002, E.P.C.N. 2007, 2008). Consequently, small waterbodies are being considered as ecologically and biologically important habitats that can contain important amounts of biodiversity and towards which more conservation policies should be developed and applied.

Urban environments represent complex ecosystems that respond to various ecological factors and anthropic stressors, but also managers and citizen's attitudes and perception, which may affect their management and viability. Consequently, to gain a better understanding of urban biodiversity patterns, as well as the structure and function of populations, communities and ecosystems in urban landscapes, these issues need to be taken into account (Pickett et al.

1997, Collins et al. 2000, Grimm et al. 2000, McDonnell and Hahs 2013). Urban ponds have been the focus of various studies, which indicate that they may have interesting biodiversity potential (Hassall 2014). However, knowledge about the ecology of certain ecologically important groups such as zooplankton is rather scarce. Consequently, we chose to carry out this study in order to obtain a better definition of zooplankton biodiversity and their sources of variation in urban waterbodies. First off, we wanted to determine biodiversity patterns as well as identify their sources of variation across eighteen waterbodies in the urban landscape of the city of Montreal. We used this information to help evaluate the biodiversity potential of urban waterbodies, as well as elucidate how these biodiversity patterns vary. Afterwards, we explored the phylogenetic diversity of cladocerans communities in waterbodies on the Island of Montreal and try to suggest ways to best preserve it. We also evaluated the consequences of phylogenetic uncertainty for identifying sites for conservation priority based on phylogenetic diversity. Finally, we studied monthly variation in community composition and feeding group patterns to see how zooplankton communities vary in time in urban waterbodies. We also attempted to explain patterns in species richness and community composition composition in order to determine determine the main drivers of zooplankton diversity in these urban waterbodies. In this section, we will discuss the main results of this study, emphasizing their originality and their importance in the general understanding of zooplankton community ecology in urban waterbodies.

5.2 Assessing aquatic biodiversity of zooplankton communities in an urban landscape

Zooplankton communities are important actors in aquatic ecosystems, playing various roles in food webs, ecosystem health and nutrient cycling. Consequently, their biodiversity

patterns should be of particular interest for aquatic biodiversity evaluations in urban ecosystems. However, of the various studies that concerned zooplankton communities in urban waterbodies, most of them concerned only separate compartments of zooplankton, such as crustaceans (Dodson et al. 2005, Dodson 2008), rotifers (Langley et al. 1995, Ejsmont-Karabin and Kuczyńska-Kippen 2001) or protists (Burdíková et al. 2012). Consequently, a coherent appraisal of zooplankton communities' biodiversity patterns in a single study is still lacking for urban ponds. Furthermore, the biodiversity and responses can differ between communities (Allen et al. 1999, Declerck et al. 2005). This means that trends and patterns obtained for one taxonomic group may not be the same for another.

In our first study, we sought to provide a general assessment of zooplankton communities in urban waterbodies by taking three of the main taxonomic groups of zooplankton (Cladocera, Copepoda and Rotifera). Across all 18 waterbodies in the urban region, a total of 80 zooplankton taxa were noted. Rotifers were the most diverse, with 45 taxa, followed by cladocerans and copepods, respectively with 26 and 9 taxa. By comparing the observed species richness in our waterbodies with other waterbodies (Appendix 2), we can get a rough idea of how diverse our urban waterbodies are. It is worth noting that, for all three considered zooplankton assemblages, urban waterbodies were never the lowest value reported. Even though such direct comparisons are hampered by important differences in the number of studied waterbodies, sampling methodology and ecological environments, they still show that urban waterbodies can represent important reservoirs of biodiversity and should therefore have a more important position in urban landscape than aesthetic pieces.

Furthermore, study of beta-diversity patterns and MANOVAs between the waterbodies and the sampling zone (pelagic and littoral) also provided interesting results that should be

taken into account by further studies or biodiversity assessments. Firstly, a negative relationship between waterbody's individual zooplankton species richness and LCBD values were found. This implies that some waterbodies, despite being poor in zooplankton taxa, contribute to important variation in community composition between sites, which would raise their profile. Second, there was a strong negative relationship between waterbodies' cladoceran and rotifer LCBD values. This relationship shows that these all zooplankton taxonomic assemblages should be sampled and have their contributions to biodiversity assessed in order to evaluate urban waterbody biodiversity. Finally, significant interactions were found when comparing zooplankton communities between waterbodies and between zones (littoral and pelagic) for three different diversity metrics. The littoral zone of waterbodies could produce sampling units which were equally rich as those of the pelagic zone or remarkably richer, up to more than twice the number of taxa. Similar patterns were also observed with multivariate diversity metrics (Jaccard dissimilarity and Hellinger distance), wherein communities between zones in waterbodies could be quite similar or very different. This implies that, even within mostly small and shallow urban waterbodies, the littoral zone of waterbodies should be considered as important for aquatic biodiversity (Walseng et al. 2006, Vadeboncoeur et al. 2011). These three results define urban waterbodies as quite complex ecosystems that show variability among each other, but also within.

Finally, in urban waterbodies, zooplankton community composition was related to a variety of environmental factors, as is the case for non-urban lakes (Pinel-Alloul et al. 1995, Beisner et al. 2006). In our study, we found that variables associated to both bottom-up (morphometry, water quality and nutrient enrichment) as well as top-down forces (macroinvertebrate predation) influenced zooplankton communities. An interesting influence

was that of management practices, as the practice of routinely draining waterbodies during winter increased the relative abundance of medium and large bodied cladocerans in these environments. Despite the similarity of this process to the natural notion of ponds drying out during the summer, attention should be paid to when waterbodies are cleaned to ensure that the water and sediments at the bottom, which contain the original community, are not disturbed. Therefore, in addition to natural environmental variation, urban waterbodies are affected by additional, anthropic stressors.

Despite being located in an urban landscape and the consequent predominant presence of anthropogenic stressors, waterbodies in Montreal play more than just a social or aesthetic role. Indeed, we have shown that they sustain noticeable amounts of aquatic biodiversity for several zooplankton groups. This would imply that urban waterbodies can represent reservoirs of urban aquatic biodiversity. Urban waterbodies constitute part of the urban landscape, which means that they will be influenced by anthropogenic factors and management practices, as we have found. Management practices favouring a large diversity of permanent and temporary habitats with littoral vegetated zones should be incorporated into urban design and conservation plans.

5.3 Phylogenetic diversity and its conservation in the presence of phylogenetic uncertainty: a case study for cladoceran communities in urban waterbodies

Ponds and small waterbodies are abundant and quite common ecosystems found in various locations such as natural and rural, but also urban environments. They can contain several rare or unique species and can contribute notably to landscape diversity (Oertli et al. 2002, Wood et al. 2003, Williams et al. 2003). Within urban environments, these waterbodies

and their communities respond to various ecological factors and anthropic stressors, but also park maintenance agents and citizen's attitudes and perception, which may affect their management and viability. Furthermore, increasing pressure due to the necessity of land for urban space and agricultural intensification have led to a considerable decline in the number ponds in some areas of the world (Wood et al. 2003, Hassall 2014). However, despite the presence of human activities and stressors, urban waterbodies can contain noticeable amounts of zooplankton biodiversity and are not poor in biodiversity (Langley et al. 1995, Ejsmont-Karabin and Kuczyńska-Kippen 2001, Mimouni et al. 2015). Consequently, they may represent important reservoirs for urban zooplankton biodiversity. It is therefore imperative to be able to assess their biodiversity value and evaluate conservation plans.

In our second study, we evaluated the phylogenetic diversity of cladoceran communities of urban waterbodies on the Island of Montreal. In addition to aiding taxonomic and biogeographical studies, molecular data can aid conservation studies by providing knowledge of species' evolutionary history (Erwin 1991, Soltis and Gitzendanner 1999, Bowen 2002). Phylogenetic diversity comprises a tool that can help incorporate species differences into conservation prioritization, and there are various ways to define and measure it (Vellend et al. 2010). During the months of June, July and August of 2011, 19 urban waterbodies on the Island of Montreal were sampled in order to determine their cladoceran communities. Using phylogenetic trees based on DNA sequences from two mitochondrial genes using a Bayesian approach, the phylogenetic diversity (PD) of cladoceran communities in these waterbodies was determined.

The sampled waterbodies differed in their phylogenetic diversity as PD values based on the maximum clade credibility tree ranged from 0.30 to 1.49. This means that there are

important differences in the amount of evolutionary history contained in urban waterbodies. However, whereas PD can be maximized in a single site in a relatively straightforward manner (Steel 2005, Hartmann and Steel 2006), for the specific case of region conservation, algorithms that can find the optimal solution can be difficult to find (Moulton et al. 2007). For each number of waterbodies that can be preserved, noticeable differences were observed between the best and worse combinations of sites PD value and often, several quite different combinations had optimal PD values. Furthermore, if the the best combination of waterbodies is chosen, the PD can be maximized using a combination of 5 waterbodies, of which there are 6 possibilities. Consequently, which sites to preserve in order to maximize PD is a rather complicated question that should be guided.

However, such a process discards an important notion, which is the fact that phylogenetic trees are probabilistically inferred rather than reported with absolute certitude. In the case of Cladocera, placing absolute confidence in a single tree would be a dangerous procedure, as the taxonomy, classification and phylogeny of the group have considerably changed over time (Fryer 1987, Korovchinsky 1997). Uncertainty in phylogenetic inference estimates is an important aspect of phylogenies and should not be disregarded. Bayesian analyses offer a method that simultaneously estimates trees and obtains measurements of uncertainty (Holder and Lewis 2003). When PD values are computed on the posterior distribution of trees, an estimation of the effect of phylogenetic uncertainty on PD evaluation can be obtained. The collections of raw values and ranks of PD computed on the posterior distribution of trees showed that, when phylogenetic uncertainty is taken into account, some of the comparisons are supported, but several are not. As a consequence, the ranking as a whole is less authoritative and prioritization of sites over others should be done with more caution.

Our study has shown that the estimation and preservation of phylogenetic diversity for cladocerans communities in urban waterbodies is a complicated issue. Furthermore, we have highlighted the importance that phylogenetic uncertainty can have on estimates of phylogenetic diversity. To some extent, the importance of incorporating phylogenetic uncertainty would depend on how robust phylogenies are for the considered group. However, phylogenetic inference is a growing field for which advances are being made both theoretically and computationally (Felsenstein 2004, Yang 2006). Therefore, we believe that the notion of phylogenetic diversity estimation should be linked to the phylogenetic inference process rather than considered a separate step. The incorporation of phylogenetic information into biodiversity studies is a worthwile task that is sure to develop in the near future. However, its relationship to the statistical aspects of model-based phylogenetic inference should be further elaborated. We have shown that phylogenetic uncertainty can affect conservation prioritization and that it should always be considered in order to avoid making wrong or suboptimal choices.

5.4 Spatio-temporal variation of community composition and feeding groups of zooplankton in urban waterbodies of a North American city

Small waterbodies such as ponds are common aquatic ecosystems found in all types of locations such as natural and rural, but also urban environments. In urban landscapes, these waterbodies may serve various socio-economic functions, including recreational activities (fishing ponds, golf course water hazards), stormwater management, natural reserves or purely aesthetic purposes. The number of ponds and the environmental heterogeneity in these waterbodies would promote high levels of biodiversity, noticeably increasing regional

diversity. Indeed, ponds have been noted to contain very diverse communities and contribute to regional diversity (Oertli et al. 2002, Wood et al. 2003, Williams et al. 2004). However, even though urban pond communities have been the focus of a range of various studies (Hassall 2014), the biodiversity and ecology of zooplankton communities in urban environments remains relatively unknown.

In our third study, we sought further our understanding of the variation in zooplankton communities by verifying specific properties about the monthly variation in zooplankton community composition and feeding group patterns in order to evaluate how zooplankton communities vary over time in urban waterbodies. Our first question related to whether or not community composition patterns between waterbodies and sampling zone (littoral or pelagic) remained the same over time. Indeed, the dynamic nature of zooplankton populations means that zooplankton communities can change over time, which makes it important to consider temporal change as well. We found that this pattern changed over time, as a significant three-way interaction was found. Most of the apparent differences in community composition seemed to be between waterbodies and between months within waterbodies. However, these changes were not the same for all waterbodies, as some showed very little differences between months, whereas others showed considerable differences.

Additionnally, we also studied zooplankton communities on the basis of feeding ecology. The presence of human populations and anthropogenic stressors can affect ecosystem biodiversity and processes in urban environments, which can be considerably different than more natural ones (Collins et al. 2000, Alberti et al. 2003, Alberti 2005, Kowarik 2011). In these situations, environmental filters may select species on the basis of individual traits, and it could be that these would have led to the development of a single feeding group composition

pattern across all waterbodies. However, zooplankton communities in urban waterbodies still showed important differences in terms of the dominant feeding groups and this dominance could change between months and sites. Microphagous rotifers, raptorial rotifers, seston-filtering cladocera and substrate-grazing cladocera were the main component of feeding group composition. The main difference in feeding group composition was between rotifer and cladocerans, which could be the result of competitive interactions between these two taxonomic assemblages (Gilbert and Stemberger 1985, Gilbert and MacIsaac 1989, MacIsaac and Gilbert 1989, 1991a, 1991b). Further distinction in feeding group communities can be made between raptorial rotifers and microphagous rotifers. Therefore, despite their location in an urban environment and the presence of anthropic stressors, zooplankton communities in urban waterbodies do not display a single type of feeding group composition pattern.

Finally, we sought to explain patterns in species richness and community composition using five environmental variables (total phosphorus concentration, surface area, mean depth, Secchi depth and macrophyte cover), which have been noted as being important for aquatic biodiversity (Jeppesen et al. 2000, Declerck et al. 2005), in order to determine determine the main drivers of zooplankton diversity in these urban waterbodies. Zooplankton species richness was found to be positively affected by macrophyte cover and by Secchi depth. This could be explained by the fact that macrophyte beds represent a structurally complex habitat, where some zooplankton species may find increased food conditions or refuge from certain predators. Indeed, for shallow lakes and ponds, macrophytes have been suggested as a key element in increasing invertebrate diversity (Scheffer et al. 2006). Macrophyte coverage was also an important variable for zoooplankton community composition patterns, being associated with several zooplankton taxa. However, contrary to species richness, community

composition patterns were affected macrophyte coverage, but also by waterbody area and total phosphorus concentrations. Therefore, the two aspects of diversity may share some similar structuring variables, but also have different ones. Furthermore, a smaller amount of variation was explained in the case of community composition than species richness.

Together, these questions show that zooplankton communities in urban waterbodies are made up of diverse assemblages that vary over several scales and over time. Additionally, they seem to respond to environmental variables, but also biotic interactions, which can lead to altenating patterns in assemblages. Based on our results, zooplankton richness in urban waterbodies is affected by a few key variables (macrophyte cover and water transparency). However, community composition patterns responded to some different variables and less of its variation was explained by the analysis. Consequently, additional environmental variables or ecological phenomena may affect species establishment and development in urban waterbodies. These notions should be considered by biodiversity assessment and conservation programmes.

5.5 Perspectives

The results of these studies represent a contribution to the knowledge of zooplankton communities in urban waterbodies and should allow for a better elaboration of biodiversity conservation in cities. Urban waterbodies are capable of harbouring noticeable amounts of aquatic biodiversity and efforts should be deployed in order to preserve this biodiversity. We have shown that zooplankton communities in urban waterbodies show considerable among-site differences in diversity and littoral zones often show more species and a different community composition than the pelagic zone. The phylogenetic diversity was also explored

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and we suggested ways to best preserve it in the presence of phylogenetic uncertainty. Finally, we evaluated what are the main sources of variation in community composition in urban waterbodies over a summer period and identified the main drivers of within-site species richness. All of these studies highlight the considerable variability that communities in urban waterbodies can show and the importance of preserving these ecosystems. It is therefore important to re-evaluate the place that these ecosystems hold within our cities. They should not only be considered as suppliers of goods and services or as aesthetic elements of the urban landscape, but also as active and quite dynamic ecological ecosystems that can contain important biodiversity.

Following these results, other studies can be considered to further our knowledge of urban waterbodies' ecology. First of all, we have considered three taxonomic assemblages of zooplankton communities, namely rotifers, cladocerans and copepods. However, protists are also a part of zooplankton communities that can play an important role in freshwater ecosystems (Sanders et al. 19984, Finlay and Esteban 1998a, 1998b, Carrick 2005) and whose inclusion would give a better understanding of urban zooplankton communities. Furthermore, the aquatic biodiversity within urban waterbodies is not limited to zooplankton and a full limnological study of the diversity other communities such as fish, macroinvertebrates, macrophytes and algal communities would help more accurately define urban waterbodies' biodiversity potential. Additionally, the biodiversity and the responses can differ between communities (Allen et al. 1999, Declerck et al. 2005), bringing the need to focus on the ecosystem as a whole. Likewise, pond conservation policies should also increase their attention to the ecology of the considered taxa, but also to the possibility of pond networks in addition to isolated ponds (Boothby 1997, 1999, 2000, Gibbs 2000, Jeffries 2005, E.P.C.N.

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2007). Consequently, the issue of connectivity of zooplankton populations, or lack thereof, between ponds in urban environments should be assessed.

Finally, ponds are emerging as important ecosystems in various aspects and efforts have been deployed to study, promote and preserve their biodiversity (Biggs et al. 2005, Oertli et al. 2005a, Oertli et al. 2005b, E.P.C.N. 2007, 2008). However, the issue of conservation in urban environments is a complex one. Indeed, when considering urban waterbodies, the attitudes and perceptions of citizens regarding these ecosystems also come into play. Therefore, an important part of urban waterbody biodiversity conservation work should be that the ecological importance of these ecosystems and of their biodiversity be disseminated not only to fellow researchers and conservation specialists, but also to the people that are implicated in its preservation.

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Appendix 1 – List and codes of the sampled zooplankton taxa along with the number of occurrences in the pelagic and littoral zones and overall in the waterbodies

Family	Code	Species	Pelagic zone	Littoral zone	Sites
Rotifera					
Asplanchnidae Eckstein, 1883	ASBR	*Asplanchna* sp. Gosse, 1850	6	5	6
Bdelloidea Hudson, 1884	BDEL	Bdelloidea spp. Hudson, 1884	1	0	1
Brachionidae Ehrenberg, 1838	BRAN	*Brachionus angularis* Gosse 1851	3	3	3
	BRCA	*Brachionus caudatus* Barrois and Daday, 1894	1	1	1
	BRQU	*Brachionus quadridentatus* Hermann, 1783	3	5	5
	KELO	*Kellicottia* sp. Ahlstrom, 1938	1	0	1
	KERA	*Keratella* sp. Bory de St. Vincent, 1822	12	10	12
	KEHI	*Keratella hiemalis* Carlin, 1943	1	0	1
	KESE	*Keratella serrulata* Ehrenberg, 1838	0	1	1
	KETE	*Keratella tecta* Gosse, 1851	1	1	1
	PLPA	*Platyias patulus* Müller, 1786	6	7	7
	PLQU	*Platyias quadricornis* Ehrenberg, 1832	7	6	10
Conochilidae Harring, 1913	CONO	*Conochiloides* sp. Hlava, 1904	2	2	3
Dicranophoridae Harring, 1913	DICR	*Dicranophorus* spp. Nitzsch, 1827	1	1	1
	ENCE	*Encentrum* spp. Ehrenberg, 1838	1	0	1
Euchlanidae Ehrenberg, 1838	EUDI	*Euchlanis* spp. Ehrenberg, 1832	3	11	11
Filiniidae Harring and Myers, 1926	FILI	*Filinia* sp. Ehrenberg, 1834	5	5	6
Gastropodidae Harring, 1913	ASEC	*Ascomorpha ecaudis* Perty, 1850	1	1	1
	GAHY	*Gastropus* sp. Imhof, 1888	1	1	1
Lecanidae Remane, 1933	LECA	*Lecane* sp. Nitzsch, 1827	6	8	8
	LEMO	*Lecane* (*Monostyla*) spp. Nitzsch, 1827	4	11	12
	LEBU	*Lecane bulla* Gosse, 1851	4	6	6
	LECR	*Lecane crepida* Harring, 1914	1	1	1
	LELE	*Lecane leontina* Turner, 1892	1	1	1
	LELD	*Lecane ludwigi* Eckstein, 1883	0	1	1
	LEQU	*Lecane quadridentata* Ehrenberg, 1832	2	7	7
	LEST	*Lecane stokesi* Pell, 1890	0	1	1
Lepadellidae Harring, 1913	COLU	*Colurella* sp. Bory de St. Vincent, 1824	0	1	1
	LEPA	*Lepadella* sp. Bory de St. Vincent, 1826	0	2	2
Mytilinidae Harring, 1913	MYVE	*Mytilina* cf. *ventralis* Ehrenberg, 1832	5	10	10

Nothomattidae Hudson and Gosse, 1886	CEPH	*Cephalodella* sp. Bory de St. Vincent, 1826	1	0	1
	NOTO	Nothomattidae spp. Hudson and Gosse, 1886	1	0	1
Philodinidae Ehrenberg, 1838	DISS	*Dissotrocha* sp. Bryce, 1910	6	9	10
Scaridiidae Manfredi, 1927	SCAR	*Scaridium* sp. Ehrenberg, 1830	2	4	5
Synchaetidae Hudson and Gosse, 1886	PLTR	*Ploesoma* cf. *truncatum* Herrick, 1885	2	2	2
	POLY	*Polyarthra* spp. Ehrenberg, 1834	11	13	14
	SYNC	*Synchaeta* spp. Ehrenberg, 1832	7	7	8
Testudinellidae Harring, 1913	TEPA	*Testudinella patina* Hermann, 1783	1	3	3
Trichocercidae Harring, 1913	TRCY	*Trichocerca cylindrica* Imhof, 1891	0	1	1
	TRLA	*Trichocerca lata* Jennings, 1894	1	1	1
	TRMU	*Trichocerca multicrinis* Kellicott, 1897	1	2	2
	TRPU	*Trichocerca pulsilla* Lauterborn, 1898	3	2	3
	TRSI	*Trichocerca similis* Wierzejski, 1893	3	3	3
Trichotriidae Harring, 1913	TRPO	*Trichotria pocillum* Müller, 1776	1	4	4
	TRTE	*Trichotria tetractis* Ehrenberg, 1830	1	3	3

Cladocera

Bosminidae Baird, 1845	BOSM	Bosminidae spp. Baird, 1845	13	12	13
Chydoridae Stebbing, 1902	ACHA	*Acroperus harpae* Baird, 1834	0	2	2
	ALAF	*Alona* cf. *affinis* Leydig, 1860	0	1	1
	ALON	*Alona* spp. Baird, 1850	4	14	15
	CARE	*Camptocercus rectirostris* Schödler, 1862	1	5	5
	CHYD	*Chydorus* spp. Leach, 1843	7	13	13
	DIHA	*Disparalona hamata* Birge, 1879	0	1	1
	GRTE	*Graptoleberis testudinaria* Fischer, 1848	0	1	1
	KULA	*Kurzia latissima* Kurz, 1874	1	5	5
	LEYQ	*Leydigia quadricornis* Kurtz, 1874	0	1	1
	PLDE	*Pleuroxus denticulatus* Birge, 1879	1	8	8
	PLPR	*Pleuroxus procurvus* Birge, 1879	2	7	7
Daphniidae Straus, 1820	CERI	*Ceriodaphnia* sp. Dana, 1853	3	8	8
	CERE	*Ceriodaphnia reticulata* Jurine, 1820	3	3	3
	DAAM	*Daphnia ambigua* Scourfield, 1947	1	1	1
	DAME	*Daphnia mendotae* Birge, 1918	2	0	2
	DAPH	*Daphnia* spp. Dana, 1853	1	1	1
	SCAP	*Scapholeberis* sp. Schoedler, 1858	6	11	11
	SIMO	*Simocephalus* sp. Schoedler, 1858	4	6	7
	SIVE	*Simocephalus vetulus* Müller, 1776	3	4	4
Ilyocryptidae Smirnov, 1992	ILYO	*Ilyocryptus* sp. Sars, 1862	0	5	5
Macrothricidae Norman and Brady, 1867	MAC1	*Macrothrix* sp2 Baird, 1843	0	1	1
	MAC2	*Macrothrix* sp1 Baird, 1843	0	1	1
Polyphemidae Baird, 1845	POPE	*Polyphemus pediculus* Linnaeus, 1761	0	2	2

Sididae Baird, 1850	DIAP	*Diaphanosoma* sp. Liévin, 1848	12	10	12
	SICR	*Sida crystallina* Müller, 1776	0	4	4
Copepoda					
Cyclopidae Dana, 1846	ACRO	*Acanthocyclops* cf. *robustus* Sars, 1863	1	5	5
	EUPE	*Eucyclops* cf. *pectinifer* Cragin, 1883	3	9	10
	MAAL	*Macrocyclops albidus* Jurine, 1820	0	8	8
	MEAM	*Mesocyclops* cf. *americanus* Dussart, 1895	0	3	3
	MEED	*Mesocyclops edax* Forbes, 1890	3	2	3
	TROP	*Tropocyclops* spp. Kiefer, 1927	2	5	5
Diaptomidae Baird, 1850	SKOR	*Skistodiaptomus oregonensis* Lilljeborg, 1889	3	2	3
	SKRE	*Skistodiaptomus reighardii* Marsh, 1895	1	1	1
	ONBI	*Onychodiaptomus birgei* Marsh, 1894	2	2	2

Appendix 2 – Table comparing the number of taxa reported in this study to other studies of urban and natural waterbodies and lakes

Study	Year	Location	Number of waterbodies	Cladocera	Rotifera	Copepoda
Mimouni et al. (this study)	2014	Montreal, Canada	18 urban waterbodies	26	45	9
Pinel-Alloul et al.	2013	47 provinces, Canada	1665 lakes	33	-	50
Escrivà et al.	2010	Teruel, Spain	2 mountainous ponds	19	39	7
Larson et al.	2009	Washington State, USA	103 montane lakes and ponds	22	45	21
Frutos and Carnevali	2008	Corrientes, Argentina	3 artificial ponds	14	45	2
Jose de Paggi et al.	2008	Santa Fe, Argentina	2 stormwater pond stations	16	39	10
Barnett and Beisner	2007	Quebec, Canada	18 lakes	25	-	14
Walseng et al.	2006	Mainland Norway	2466 lakes	77	-	43
Pinto-Coelho et al.	2005	Ontario and Quebec, Canada	5 small lakes and 38 headwater lakes	27	-	25
Pinto-Coelho et al.	2005	Alberta, Canada	12 shallow lakes	16	-	10
Pinto-Coelho et al.	2005	Florida, USA	5 lakes (1 with two basins)	16	-	5
Dodson et al.	2005	Wisconsin, USA	73 small and shallow lakes	25?	-	22
Serrano and Fahd	2005	Doñana National Park, Spain	19 temporary ponds	27	47	16
Duggan et al.	2001	North Island, New Zealand	33 lakes	-	79	-
Ejsmont-Karabin and Kuczyńska-Kippen	2001	Poznań, Poland	19 urban waterbodies	-	114	-
Pinel-Alloul et al.	1990	Quebec, Canada	54 lakes	12	14	9
Chengalath and Koste	1987	British Columbia and Yukon, Canada	90 ponds and lakes	-	97	-

Appendix 3 – List of species used in the phylogenetic study and their GenBank accession numbers

Species	COI	16SrRNA
Anaspides tasmaniae	DQ310660	DQ310700
Branchinecta paludosa	AF209064	AF209055
Eubranchipus sp.	AF209061	AF209052
Parartemia contracta	AF209059	AF209048
Thamnocephalus platyurus	AF209066	AF209057
Caenestheriella setosa	DQ310628	DQ310668
Caenestheriella sp.	DQ310629	DQ310669
Limnadia sp.	DQ310630	DQ310670
Lynceus sp1	DQ310626	DQ310666
Lynceus sp2	DQ310627	DQ310667
Lepidurus couesii	DQ310622	DQ310662
Triops australiensis	DQ310624	DQ310664
Triops sp.	DQ310623	DQ310663
Cyclestheria hislopi	DQ310631	DQ310671
Leptodora kindtii	DQ310659	DQ310699
Bythotrephes cederstroemi	DQ310655	DQ310695
Cercopagis pengoi	AF320013	AY075067
Evadne spinifera	DQ310656	AY075071
Pleopis polyphemoides	AY075050	AY075072
Podon leuckarti	AY075051	AY075073
Polyphemus pediculus	AY075048	AY075066
Diaphanosoma sp.	DQ310658	DQ310697
Holopedium gibberum	AF245354	DQ310698
Sida crystalline	DQ310657	DQ310696
Acroperus harpae	DQ310648	DQ310688
Alona setulosa	DQ310646	DQ310686
Bosmina sp1	DQ310635	DQ310675
Camptocercus rectirostris	DQ310647	DQ310687
Ceriodaphnia sp.	DQ310634	DQ310674
Chydorus brevilabris	DQ310642	DQ310682
Daphnia ambigua	AF523687	AF064188
Daphnia galeata	EF375868	AF064187
Daphnia pulex	NC_000844	DQ470571

Drepanothrix dentate	DQ310641	DQ310681
Eurycercus glacialis	DQ310652	DQ310692
Eurycercus longirostris	DQ310651	DQ310691
Graptoleberis testudinaria	DQ310649	DQ310689
Ilyocryptus sp.	DQ310638	DQ310678
Kurzia media	KC617023	NA
Leydigia lousi Mexicana	EU702187	NA
Macrothrix sp.	DQ310640	NA
Moina sp1	DQ310653	DQ310693
Ophryoxus gracilis	NA	DQ310677
Pleuroxus denticulatus	DQ310644	DQ310684
Pleuroxus procurvus	JN233955	NA
Saycia cooki	DQ310650	DQ310690
Scapholeberis rammneri	DQ310632	DQ310672
Simocephalus vetulus	DQ310633	DQ310673

Appendix 4 – List of cladoceran taxa with their occurrences over the summer period and each considered month

Taxa	Number of occurences Summer	Number of occurences June	Number of occurences July	Number of occurences August
Bosminidae spp. Baird, 1845	17	16	15	13
Acroperus harpae Baird, 1834	1	1	1	1
Alona spp. Baird, 1850	15	14	13	13
Camptocercus rectirostris Schödler, 1862	6	6	4	2
Chydorus spp. Leach, 1843	18	18	15	13
Eurycercus cf. *longirostris* Hann, 1982	2	2	0	0
Graptoleberis testudinaria Fischer, 1848	3	3	2	2
Kurzia latissima Kurz, 1874	5	3	1	1
Leydigia quadricornis Kurtz, 1874	2	1	1	0
Pleuroxus denticulatus Birge, 1879	10	8	7	5
Pleuroxus procurvus Birge, 1879	10	9	5	6
Ceriodaphnia sp. Dana, 1853	15	13	12	11
Daphnia ambigua Scourfield, 1947	1	1	0	0
Daphnia mendotae Birge, 1918	3	3	3	2
Daphnia spp. Dana, 1853	4	4	1	0
Scapholeberis sp. Schoedler, 1858	15	14	11	9
Simocephalus sp. Schoedler, 1858	15	14	10	10
Ilyocryptus sp. Sars, 1862	3	2	1	0
Leptodora kindtii Focke, 1844	1	1	0	0
Macrothrix sp. Baird, 1843	7	4	4	2
Ophryoxus gracilis Sars, 1861	1	0	0	1
Polyphemus pediculus Linnaeus, 1761	2	2	1	1
Diaphanosoma sp. Liévin, 1848	15	13	15	12
Sida crystallina Müller, 1776	8	6	4	5

Appendix 5 – List of recorded zooplankton taxa with their number of occurrences and their associated feeding group

Family	Code	Taxa	OccSummer	OccJune	OccJuly	OcAugust	Feeding group
Rotifera							
Asplanchnidae Eckstein, 1883	ASPL	*Asplanchna* cf. *brightwelli* Gosse, 1850	11	6	8	6	RRotifera
Atrochidae Harring, 1913	CUVO	*Cupelopagis vorax* Leidy, 1857	1	0	1	0	RRotifera
Bdelloidea Hudson, 1884	BDEL	Bdelloidea spp. Hudson, 1884	12	5	10	6	MRotifera
Brachionidae Ehrenberg, 1838	BRAC	*Brachionus* sp. Pallas, 1766	5	3	3	2	MRotifera
	BRAN	*Brachionus angularis* Gosse 1851	6	3	5	4	MRotifera
	BRCA	*Brachionus caudatus* Barrois and Daday, 1894	1	1	0	1	MRotifera
	BRQU	*Brachionus quadridentatus* Hermann, 1783	6	4	5	5	MRotifera
	KELO	*Kellicottia longispina* Kellicott, 1879	2	2	0	0	MRotifera
	KERA	*Keratella* sp. Bory de St. Vincent, 1822	19	18	17	16	MRotifera
	KEFA	*Keratella cochlearis faluta* Ahlstrom, 1943	2	1	0	1	MRotifera
	KEHI	*Keratella hiemalis* Carlin, 1943	3	3	0	0	MRotifera
	KETE	*Keratella tecta* Gosse, 1851	3	3	2	2	MRotifera
	NOAC	*Notholca acuminata* Ehrenberg, 1832	3	3	0	0	MRotifera
	NOEX	*Notholca acuminata extensa* Ehrenberg, 1832	1	1	0	0	MRotifera
	PLPA	*Platyias patulus* Müller, 1786	12	7	9	10	MRotifera
	PLQU	*Platyias quadricornis* Ehrenberg, 1832	4	3	1	2	MRotifera
Conochilidae Harring, 1913	CONO	*Conochiloides* sp. Hlava, 1904	6	2	2	4	MRotifera
Dicranophoridae Harring, 1913	DICR	*Dicranophorus* sp. Nitzsch, 1827	9	2	5	8	RRotifera
Euchlanidae Ehrenberg, 1838	EUCH	*Euchlanis* spp. De Beauchamp, 1910	16	12	13	12	MRotifera
Filiniidae Harring and Myers, 1926	FILI	*Filinia* sp. Bory de St. Vincent, 1824	9	3	7	6	MRotifera
Gastropodidae Harring, 1913	ASEC	*Ascomorpha ecaudis* Perty, 1850	11	6	9	5	RRotifera
	GAHY	*Gastropus* cf. *hyptopus* Ehrenberg, 1838	2	2	1	1	RRotifera
Hexarthridae Bartos, 1959	HEMI	*Hexarthra mira* Hudson, 1871	6	2	5	5	MRotifera
Lecanidae Remane, 1933	LECA	*Lecane* sp. Nitsczh, 1827	14	7	11	11	MRotifera
	LEMO	*Lecane* (*Monostyla*) sp. Nitzsch, 1827	18	16	15	12	MRotifera
	LEBU	*Lecane* (*Monostyla*) *bulla* Gosse, 1851	15	11	9	10	MRotifera
	LECR	*Lecane crepida* Harring, 1914	2	0	0	2	MRotifera
	LELE	*Lecane leontina* Turner, 1892	2	1	1	1	MRotifera
	LELU	*Lecane ludwigi* Eckstein, 1883	3	1	1	2	MRotifera
	LEOH	*Lecane ohioensis* Herrick, 1885	6	4	4	2	MRotifera
	LEQU	*Lecane* (*Monostyla*) *quadridentata* Ehrenberg, 1832	10	7	9	8	MRotifera

	LEST	*Lecane stokesi* Pell, 1890	2	2	0	1	MRotifera
Lepadellidae Harring, 1913	COLU	*Colurella* sp. Bory de St. Vincent, 1824	7	5	5	7	MRotifera
	LEPA	*Lepadella patella* Bory de St. Vincent, 1826	13	11	9	8	MRotifera
	LEEH	*Lepadella ehrenbergi* Perty 1850	3	0	2	3	MRotifera
	PARA	*Paracolurella* sp. Myers, 1936	1	1	0	0	MRotifera
Mytilinidae Harring, 1913	LOPH	*Lophocharis* sp. Ehrenberg, 1838	3	3	0	0	MRotifera
	MYTI	*Mytilina* sp. Bory de St. Vincent, 1826	11	9	10	5	MRotifera
Nothomattidae Hudson and Gosse, 1886	NOTH	Nothomattidae spp. Hudson and Gosse, 1886	2	1	1	0	RRotifera
	CEGI	*Cephalodella gibba* Ehrenberg, 1832	9	3	5	7	RRotifera
	MONO	*Monommata* sp. Bartsch, 1870	3	2	0	2	RRotifera
Philodinidae Ehrenberg, 1838	DISS	*Dissotrocha* sp. Bryce, 1910	8	7	7	7	MRotifera
Scaridiidae Manfredi, 1927	SCAR	*Scaridium* sp. Ehrenberg, 1830	5	4	3	4	RRotifera
Synchaetidae Hudson and Gosse, 1886	PLOE	*Ploesoma* sp. Herrick, 1885	3	1	2	3	RRotifera
	POLY	*Polyarthra* spp. Ehrenberg, 1834	17	13	16	15	RRotifera
	POEU	*Polyarthra* cf. *euryptera* Wierzejski, 1891	1	1	0	0	RRotifera
	SYN	*Synchaeta* spp. Ehrenberg, 1832	10	6	4	7	RRotifera
	POSU	*Pompholyx sulcata* Hudson, 1885	1	1	0	1	MRotifera
Testudinellidae Harring, 1913	TEST	*Testudinella* sp. Bory de St. Vincent, 1826	13	9	11	8	MRotifera
	TRIC	*Trichocerca* sp. Lamarck, 1801	1	0	1	0	RRotifera
Trichocercidae Harring, 1913	TRBI	*Trichocerca bicristata* Gosse, 1887	9	4	5	7	RRotifera
	TRCY	*Trichocerca cylindrica* Imhof, 1891	6	6	4	4	RRotifera
	TRLA	*Trichocerca lata* Jennings, 1894	2	0	2	2	RRotifera
	TRMU	*Trichocerca mucosa* Stokes, 1896	6	5	2	2	RRotifera
	TRMC	*Trichocerca multicrinis* Kellicott, 1897	4	1	1	4	RRotifera
	TRRA	*Trichocerca rattus* Müller, 1776	2	2	0	0	RRotifera
	TRSI	*Trichocerca similis* Wierzejski, 1893	7	4	5	5	RRotifera
Trichotriidae Harring, 1913	MACR	*Macrochaetus* sp. Perty, 1850	1	1	0	0	MRotifera
	TRPO	*Trichotria pocillum* Müller, 1776	10	7	5	7	MRotifera
	TRTE	*Trichotria tetractis* Ehrenberg, 1830	7	5	5	2	MRotifera
Cladocera							
Bosminidae Baird, 1845	BOSM	Bosminidae spp. Baird, 1845	17	16	15	13	SFCladocera
Chydoridae Stebbing, 1902	ACHA	*Acroperus harpae* Baird, 1834	1	1	1	1	SGCladocera
	ALON	*Alona* spp. Baird, 1850	15	14	13	13	SGCladocera
	CARE	*Camptocercus rectirostris* Schödler, 1862	6	6	4	2	SGCladocera
	CHYD	*Chydorus* spp. Leach, 1843	18	18	15	13	SGCladocera
	EURY	*Eurycercus* sp. Baird, 1843	2	2	0	0	SGCladocera
	GRTE	*Graptoleberis testudinaria* Fischer, 1848	3	3	2	2	SGCladocera
	KULA	*Kurzia* cf. *latissima* Kurz, 1874	5	3	1	1	SGCladocera
	LEAC	*Leydigia* cf. *acanthocercoides* Fischer, 1853	2	1	1	0	SGCladocera
	PLDE	*Pleuroxus denticulatus* Birge, 1879	10	8	7	5	SGCladocera

	PLPR	*Pleuroxus procurvus* Birge, 1879	10	9	5	6	SGCladocera
Daphniidae Staus, 1820	CERI	*Ceriodaphnia* sp. Dana, 1853	15	13	12	11	SFCladocera
	DAAM	*Daphnia ambigua* Scourfield, 1947	1	1	0	0	SFCladocera
	DAGA	*Daphnia galeata mendotae* Birge, 1918	3	3	3	2	SFCladocera
	DAPU	*Daphnia* spp. Dana, 1853	4	4	1	0	SFCladocera
	SCAP	*Scapholeberis* sp. Dumont and Pensaert, 1983	15	14	11	9	SFCladocera
	SIMO	*Simocephalus* sp. Schoedler, 1858	15	14	10	10	SFCladocera
Ilyocryptidae Smirnov, 1992	ILYO	*Ilyocryptus* sp. Sars, 1862	3	2	1	0	SGCladocera
Leptodoridae Lilljeborg, 1861	LEKI	*Leptodora kindtii* Focke, 1844	1	1	0	0	CCladocera
Macrothricidae Norman and Brady, 1867	MACR	*Macrothrix* sp. Baird, 1843	7	4	4	2	SGCladocera
	OPGR	*Ophryoxus gracilis* Sars, 1861	1	0	0	1	SGCladocera
Polyphemidae Baird, 1845	POPE	*Polyphemus pediculus* Linnaeus, 1761	2	2	1	1	CCladocera
Sididae Baird, 1850	DIAP	*Diaphanosoma* sp. Fischer, 1850	15	13	15	12	SFCladocera
	SICR	*Sida crystallina* Müller, 1776	8	6	4	5	SGCladocera
Copepoda							
Cyclopidae Dana, 1846	EUPE	*Eucyclops* cf. *pectinifer* Cragin, 1883	10	6	8	8	RCopepoda
	MAAL	*Macrocyclops albidus* Jurine, 1820	8	6	6	2	RCopepoda
	MICR	*Microcyclops* sp. Claus, 1893	11	4	8	8	RCopepoda
Diaptomidae Baird, 1850	SKRO	*Skistodiaptomus oregonensis* Lilljeborg, 1889	3	3	3	2	SSFCopepoda
	SKRE	*Skistodiaptomus reighardii* Marsh, 1895	5	2	5	1	SSFCopepoda
	ONBI	*Onychodiaptomus birgei* Marsh, 1894	6	5	1	0	SSFCopepoda