

Phylogenetic, taxonomic, and functional diversity of wetland Diptera communities

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TABLE OF CONTENTS

LIST OF TABLES	v
LIST OF FIGURES	v
LIST OF APPENDICES	vii
ABSTRACT	ix
RÉSUMÉ	xi
PREFACE	xiii
ACKNOWLEDGMENTS	xv

CHAPTER 1: Introduction and literature review

1.1. INTRODUCTION	1
1.2. LITERATURE REVIEW	3
1.2.1. CONCEPTS	3
1.2.1.1. Community analysis	3
1.2.1.2. Phylogenetic structure	3
1.2.1.3. Functional traits	4
1.2.1.4. Landscape structure	4
1.2.1.5. Scales	5
1.2.2. STUDY HABITATS AND ORGANISMS	6
1.2.2.1. Wetlands in Canada	6
1.2.2.2. Arthropods in wetlands	8
1.2.2.3. Ecological diversity of wetland Diptera	9
1.2.2.4. Diptera phylogenetic relationships	9
1.3. OBJECTIVES	11
1.4. HYPOTHESES AND PREDICTIONS	12
1.5. REFERENCES	13
1.6. CONNECTING STATEMENT	23

CHAPTER 2: Effect of habitat type on taxonomic, phylogenetic and functional diversity of wetland Diptera

2.1. ABSTRACT.....	24
2.2. INTRODUCTION	25
2.3. MATERIALS AND METHODS	28
2.4. STATISTICAL ANALYSES	29
2.4.1. Diptera diversity and community structure	29
2.4.2. Phylogeny reconstruction	31
2.4.3. Phylogenetic and functional community structure	32
2.4.4. Phylobetadiversity	33
2.5. RESULTS.....	34
2.5.1. Alpha taxonomic structure.....	34
2.5.2 Beta taxonomic structure	35
2.5.3. Alpha phylogenetic structure	35
2.5.4. Beta phylogenetic structure	36
2.6. DISCUSSION	37
2.6.1. Taxonomic structure	37
2.6.2. Phylogenetic structure	38
2.6.3. Taxonomic vs phylogenetic structure	40
2.6.4. Rarity effect	41
2.7. CONCLUSIONS AND CONSERVATION IMPLICATIONS	42
2.8. ACKNOWLEDGMENTS.....	43
2.9. REFERENCES	43
2.10. CONNECTING STATEMENT	64

CHAPTER 3: Latitudinal patterns in phylogenetic and functional diversity of Diptera in temperate bogs

3.1. ABSTRACT.....	65
3.2. INTRODUCTION	65
3.3. MATERIALS AND METHODS	69
3.3.1. Study sites, sampling and processing	69
3.3.2. Habitat and vegetation variables.....	70
3.4. STATISTICAL ANALYSES	71

3.4.1. Taxonomic and functional composition.....	71
3.4.2. Phylogeny reconstruction	72
3.4.3. Phylogenetic community structure	74
3.4.4. Phylogenetic signals in trait diversity.....	74
3.5. RESULTS.....	76
3.5.1. Species and functional alpha and beta diversity	76
3.5.2. Phylogenetic alpha and beta composition.....	77
3.6. DISCUSSION	79
3.7. CONCLUSIONS.....	82
3.8. ACKNOWLEDGMENTS.....	83
3.9. REFERENCES	84

CHAPTER 4: General discussion, conclusion and future directions

4.1. INTRODUCTION	108
4.2. SUMMARY OF RESEARCH	108
4.2.1. Phylogenetic and taxonomic responses of Diptera communities to wetland habitats	108
4.2.2. Spatial patterns of taxonomic, functional and phylogenetic structure in peatlands	109
4.3. SYNTHESIS AND RECOMMENDATIONS FOR FUTURE WORK..	109
4.4. REFERENCES	111
5. APPENDICES: Supplementary materials for Chapter 2 and 3.....	113

LIST OF TABLES

- Table 2.1.** Ground cover variables reduced with principal component analysis. Variables with loadings larger than 0.32 in principal components (PC) 1 to 4 are in bold 55
- Table 2.2.** Abundance (N), species richness (S_{obs}) and rarefied species richness \pm standard error (S_{est}) for each of the 12 wetland sites. Rarefied species richness was standardized at 196 individuals (PIN_BG) 57
- Table 3.1.** Life-history and ecological traits considered in this study including categories, abbreviations and trait determination notes. Traits were assigned at the species level and adult stage except for feeding habits and specialization (larval stage)98
- Table 3.2.** Abundance (Abun), observed species richness (S), Chao1 indices (Chao1), rarefied species richness (Srare), functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) for all sites and mean diversity for each ecoregion100
- Table 3.3.** Dominant functional composition of each site, represented by community-level weighted means (CWM). For continuous traits the mean trait value is weighted by abundance, while for categorical traits the dominant class is returned. For description of traits and associated codes refer to table 3.1101
- Table 3.4.** Phylogenetic diversity (PD), net relatedness index (NRI) and nearest taxon index (NTI) for Diptera communities in 15 sites across three ecoregions at three spatial scales (trap, site, ecoregion). Fisher’s combined probability tests were performed to assess if overall *P*-values were significant at the trap and site scales. Null models were used at the ecoregion scale to assess if communities were significantly different from random. Significant *p*-values are in bold font102

LIST OF FIGURES

- Figure 2.1.** Map of the 12 study locations in the Montreal metropolitan area and surroundings, Quebec, Canada. Stars: swamps; squares: marshes; triangles: bogs. (CAL_SW: Pointe-Calumet

swamp; TIH_SW: St-Thimothé swamp; OKA_SW: Oka National Park swamp; LAZ_SW: St-Lazare swamp; BER_MA: Ile St-Bernard marsh; OKA_MA: Oka National Park marsh; MIL_MA: Mirabel Parc du Domaine Vert marsh; FOR_MA: Pointe-Fortune marsh; BLA_BG: Blainville bog; PIN_BG: Pin-Rigide bog; BRB_BG: Ste-Barbe Large Tea Field bog; MIR_BG: Mirabel bog). Map created with SimpleMappr (www.simplemappr.net) 58

Figure 2.2. Hypothesized phylogenetic relationships, based on CO1, among Schizophora (Diptera) species collected in the 12 wetlands. Colours represent families, branch lengths represent divergence time estimates and numbers on nodes represent posterior probabilities. Species codes are in Appendix 2.3..... 59

Figure 2.3. Non metric multidimensional scaling ordination of Diptera species collected A) by week in each wetland type and B) overall in the three types of wetlands. Arrows represent vectors of the seven variables that explain Diptera species composition 60

Figure 2.4. Changes in A) Trophic mean abundance and richness; B) Rarity mean abundance and richness; and C) Size class mean abundances and richness of Diptera between bogs (BG), marshes (MA) and swamps (SW) 61

Figure 2.5. Distribution of mean \pm standard deviation of phylogenetic diversity, net relatedness index (NRI) and nearest taxon index (NTI) of Diptera across the three wetland types (BG: bog, MA: marsh, SW: swamp). * Significant deviation from 0 (t-test) at $p < 0.05$ 62

Figure 2.6. Non metric multidimensional scaling ordination of species and trait phylogenetic beta diversity of mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) of Diptera in the three types of wetlands. Arrows represent vectors of the variables that explain phylogenetic turnover in community composition 63

Figure 3.1. Map of the 15 study peatland sites across Quebec, Canada. Map is separated into ecoregions: Montreal - Eastern Great Lakes Lowland Forest; Saguenay - Eastern Canadian

Forest; James Bay - Central Canadian Shield (Ricketts and Himhoff 2003). Map created with SimpleMappr (www.simplemappr.net)..... 103

Figure 3.2. Relationship between Diptera species functional traits and environmental/climatic variables revealed by fourth-corner analysis. Blue cells correspond to negative significant relationships; red cells correspond to positive significant relationships.....104

Figure 3.3. Redundancy analyses of species (A) and functional composition (B). Arrows represent vectors of significant variables ($p < 0.05$) explaining community structure, R-squared values in parentheses from the forward-selected models examining the effect of environmental factors..... 105

Figure 3.4. Redundancy analyses of beta phylogenetic composition for mean nearest taxon distance MNTD (A) and mean pair-wise distance MPD (B). Arrows represent vectors of significant variables ($p < 0.05$) explaining community structure, R-squared values in parentheses from the forward-selected models examining the effect of environmental factors 106

Figure 3.5. Variation partitioning diagrams of taxonomic (BetaTD), functional (BetaFD) and phylogenetic (BetaMNTD, BetaMPD) composition. Circles represent variation explained by unique and shared fractions of significant (based on forward selection) environmental, climatic and spatial variables, while numbers correspond to the adjusted coefficient of determination (adjusted R^2) associated to each circle. Only significant and positive adjusted R^2 are shown 107

LIST OF APPENDICES

Appendix 2.1. Traits assigned to each Schizophora species and morphospecies collected from each of the 12 wetland sites. Species in grey were excluded from analyses. (NA = unknown) 113

Appendix 2.2. Coordinates, surrounding landscape, local and chemical variables and ground cover attributes at each of the 12 wetland sites. Water table level was determined following these categories: 1. Water level below surface, 2. Water level at surface, 3. Water level less than 1 m above surface, 4. Water level more than 1 m above surface 124

Appendix 2.3. Abundance of Schizophora species and morphospecies collected from each of the 12 wetland sites. Species in grey were excluded from analyses 128

Appendix 3.1. Abundance of Diptera species and morphospecies in the 15 bogs sites across the three ecoregions 137

Appendix 3.2. Traits assigned to each Diptera species and morphospecies collected from the 15 bog sites in the three ecoregions. Refer to table 3.1 for an explanation of each trait and code (NA = unknown) 143

Appendix 3.3. Coordinates, local variables, landscape variables and climate variables in the 15 bog sites across the three ecoregions. Water table level was determined following these categories: 1. Water level below surface, 2. Water level at surface, 3. Water level above surface 150

Appendix 3.4. Ground cover variables reduced with principal component analysis. Principal components (PC) 1 to 5 were identified as significant using the Kaiser-Guttman criterion (Yeomans and Golder 1982). Variables with the largest loadings are in bold and were forming the clusters of interest 153

ABSTRACT

The goal of this thesis was to describe biodiversity and community composition of Diptera in wetlands across Quebec. Three approaches to community analysis were used to describe patterns: taxonomic identity, functional traits, and phylogenetic relationships. Diptera were sampled using standardized methods (pan traps, sweeping) across three types of wetlands (marsh, swamp, bog) in the Montreal region, and in 15 bogs distributed in three Quebec ecoregions.

When comparing three types of wetlands, abundance and species richness did not differ even with wetland areas ranging from 6 to 161 ha. Bogs supported phylogenetically closely related Diptera species filtered by harsher environmental conditions compared to the other two wetland types. Clustering of closely related species was found in bogs, which is probably due to environmental filtering at the initial stage of community assembly postglacially. The slow peat accumulation process and characteristic plant composition adapted to acidic and low nutrient conditions potentially play a role in the structure of the Diptera community. Neutral processes were more important in marshes and swamps, as dispersal limitation explained species abundance dynamics of small and common Diptera species within each wetland type. The assembly of marsh communities is a balance between neutral processes and environmental filtering, while the assembly of swamp habitats is neutral. Clustering, thus environmental filtering, increased with environmental extremes. Rare species tended to be distantly related to common species, based on phylogenetic signal. They have unique habitat requirements and their diversity is maintained by temporal turnover during the active season of species with similar traits filtered by the environment.

When the spatial extent of the research was expanded to bogs in three Quebec ecoregions, a selective filtering role of anthropogenic disturbance was found. Recent drastic human modification of the landscape in Eastern Great Lakes Lowland Forest ecoregion, less suitable peatland patches and more barriers to dispersal are adjacent to those bogs, so agriculture and urban development act as filters for the small proportion of species in the regional pool that can disperse in these conditions. In Eastern Canadian Forest and Central Canadian Shield ecoregions, stochastic processes such as dispersal limitation of abundant, small, multivoltine species seem to

be the dominant influence. High diversity of Diptera species and different historical disturbances are at the origin of the functional and phylogenetic structure observed for peatland Diptera.

Phylogenetic community structure and functional analyses revealed high value and complementarity to standard biodiversity measures. Using only traditional metrics, it would not have been apparent that bog communities are impacted by land-use changes and that these impacts change the species pool capable of inhabiting these isolated habitats. This suggests that the three levels of diversity studied should be used in environmental assessments to have a complete picture of macroecological patterns in wetlands. Conservation of mobile organisms in wetlands will depend on conservation plans focusing on both patch quality and surrounding landscape. Different conservation strategies need to be applied in the different ecoregions.

RÉSUMÉ

L'objectif de cette thèse était de décrire les patrons de biodiversité et la composition des communautés de diptères dans les milieux humides du Québec. Trois facettes de la diversité ont été utilisées : taxonomique, fonctionnelle et phylogénétique. Les diptères ont été collectés selon des méthodes standardisées dans trois types de milieux humides (marais, marécage, tourbière) dans la région de Montréal et alentours et dans 15 tourbières distribuées dans trois écorégions du Québec.

Entre les trois types de milieux humides comparés, l'abondance et la richesse en espèces n'étaient pas significativement différentes et ne changeaient pas non plus avec la variation de la superficie qui s'étendait de 6 à 161 ha. Les tourbières supportent des espèces proches phylogénétiquement, probablement dû au filtrage environnemental au début de la colonisation post glaciaire. Cette structure a probablement été causée par le très long processus d'accumulation de la tourbe et une composition caractéristique des plantes adaptées aux conditions acide et pauvre en nutriments. Les processus neutres étaient plus importants dans les marais et marécages, la limitation de la dispersion expliquait la dynamique d'abondance des espèces petites et communes. L'assemblage des communautés des marais sont le résultat d'un équilibre entre les processus neutres et de niche, tandis que l'assemblage des marécages n'est le résultat que de processus neutres. L'agrégation phylogénétique, donc le filtrage environnemental augmente avec les conditions extrêmes des marécages, aux marais, aux tourbières. Les espèces rares ont tendance à être éloignées phylogénétiquement des espèces communes, étant donné qu'un signal phylogénétique a été trouvé. Les espèces rares ont des exigences environnementales uniques et leur grande diversité est maintenue par une rotation dans le temps d'espèces ayant des traits fonctionnels similaires pendant la saison active.

L'étude des communautés de diptères des tourbières dans trois écorégions du Québec a découvert un rôle de filtre sélectif aux perturbations anthropiques. Les modifications drastiques d'origine humaine du paysage, dont l'agriculture et l'urbanisation, dans l'écorégion des Forêt des Basses-Terres de l'Est des Grands Lacs, ainsi que les conditions moins favorables des fragments de tourbières restants et les barrières à la dispersion sont responsables du filtrage de la petite proportion d'espèces pouvant s'installer dans ces tourbières isolées. Dans les écorégions des

Forêts de l'Est et du Bouclier Central, les processus aléatoires prédominent, notamment la limitation de la dispersion des espèces abondantes, petites et multivoltines. La grande diversité des diptères et les différentes perturbations historiques semblent être à l'origine de la structure fonctionnelle et phylogénétique des diptères présents dans les tourbières.

Les structures phylogénétique et fonctionnelle des communautés se sont révélées d'une grande valeur et complémentaires aux mesures de biodiversité standards. Si nous avons utilisé seulement des indices traditionnels, nous aurions manqué l'impact des changements dans l'utilisation des terres environnantes et que ces impacts influencent les espèces capable d'habiter ces sites uniques et isolés. Donc, ceci suggère que ces trois facettes de la diversité devraient être utilisées lors d'évaluations environnementales pour obtenir un portrait complet des patrons macroécologiques dans ces milieux menacés. Les résultats montrent que la conservation des organismes mobiles dans les milieux humides dépendra des plans de conservation focusant à la fois sur la qualité du fragment et du milieu environnant. Des stratégies de conservation différentes doivent être appliquées dans ces trois écorégions.

PREFACE

This is a manuscript-based thesis. Chapter 2 and Chapter 3 will be submitted to peer-reviewed journals. Chapter 2 is formatted for submission to *Ecography*. Chapter 3 is formatted for submission to *Journal of Animal Ecology*. Because Chapter 2 and 3 arise from similar field studies, there is some repetition in methods so that each manuscript can stand alone. Chapter 1 introduces the thesis and its objectives, and provides a literature review. Chapter 4 summarizes the main findings of the research and general conclusions, and provides recommendations for future directions.

Contribution of authors

I designed the study and performed all Diptera sampling described in Chapter 2. I identified most Diptera specimens. I prepared specimens for DNA barcoding and carried out all phylogenetic analyses. I selected and conducted all statistical analyses. I wrote all original manuscripts. Dr. Terry A. Wheeler participated actively in the development of the research design, identification and verification of Chloropidae and Sphaeroceridae and editing of manuscripts. He is a co-author on manuscripts from Chapter 2 and 3.

Contributions to knowledge

- Over 8000 specimens of Diptera, including rare, new species and new species records, have been curated and deposited in the largest university insect collection of Canada.
- This study helped to characterize the diversity, distribution, ecological roles, and conservation status of Diptera in pristine and fragmented wetlands.
- This study used newly generated phylogenetic trees of over 200 species of wetland Diptera to analyse phylogenetic structure in community assembly.
- This study is one of the few to use a highly diverse insect group in the context of community phylogenetics and the first study of community phylogenetics in a diverse community of Diptera.

- This study provides practical information for wetland restoration and conservation purposes in three regions of Quebec.
- This study shows that the three dominant wetland types in North America support similar Diptera abundance and species richness, regardless of the size of the wetland.
- This study shows that anthropogenic disturbances play major roles in phylogenetic and functional patterns found in peatland fly communities.
- This study shows that wetland habitats support a rich and unique insect fauna that reflects environmental changes in their phylogenetic and functional structure, making them ideal taxa for conservation and restoration monitoring.

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CHAPTER 1: Introduction and literature review

1.1. INTRODUCTION

Ecology deals with the relationships and interactions between organisms and their environment, many of which are familiar interactions, phenomena, and species we encounter every day, such as birds, trees, bees, rivers, forests, mountains, etc. However, Allen and Hoekstra (1992) noted that it would be “a mistake to imagine that this familiarity makes ecology an easy pursuit”. More than twenty years ago, Palmer (1994) compiled a list of more than 120 hypotheses predicting drivers of species diversity and undoubtedly this list would be even longer today. What drives turnover of species across space and time is one of the oldest questions in ecology and no general consensus has arisen to explain the patterns observed. Several alternative theories have been proposed. The niche theory dates back to Grinnell (1924) who defined an "ecological or environmental niche" as the distributional unit where a species can live. A few years later, Elton (1927) developed a concept of niche in terms of food habits of a species. Later, Hutchinson (1957) defined the notion of ecological niche as a multidimensional space of suitable environmental variables for the survival of a species. More recently, Webb (2000) and Cavender-Bares et al. (2006) incorporated the phylogenetic structure of a community into ecological deterministic processes in the niche model that influence the community pattern. The concept of neutral theory developed by Bell (2001) and Hubbell (2001) assumes an equivalence between individuals (i.e. differences have no functional significance) and stochastic processes in species co-existence such as birth, death, speciation and dispersal. The continuum hypothesis (Gravel et al. 2006) proposed to unify the niche and neutral models, where the importance of deterministic and stochastic processes varies along a continuum. The model focuses on local community scale, where recruitment is a lottery between species competitive ability (niche processes) and dispersal limitations (neutral processes). Another dynamic model (Jabot et al. 2008) proposed a mathematical framework in which to measure the recruitment limitation defined as the influence of dispersal limitation and post-dispersal filtering of species. Vellend (2010) organized the large number of ecological theories into four distinct processes to provide a general conceptual framework in community ecology: selection, drift, speciation and dispersal. Due to variation in species traits, and local interactions between species and their environment, selection will gradually cause changes in communities. Local-scale species composition and diversity is

recognized to derive from processes at broader spatial and temporal scales selecting species in the regional species pool. The species pool is influenced by speciation for the appearance of new species. Demographic stochasticity (i.e. ecological drift) can also play a major role in species diversity and composition changes. Movement of species between different local communities can influence community patterns at multiple scales.

Mechanistic aspects of biodiversity are now studied with a variety of approaches. The taxonomic identity approach became most popular and quantitative in the late 20th century where studies tended to focus on a single trophic level to relate biodiversity to functions (Hooper et al. 2002). Limitations of this approach have been criticized and recently functional-group and community phylogenetic approaches are more frequently used to provide new insights and opportunities. One of the most significant challenges to a taxonomic identity approach is that several diverse and ecologically important taxa are difficult (or impossible) to identify to the species level because of taxonomic uncertainty, which limits analysis of community composition. A functional classification of species into groups with similar physiological or ecological traits provides the opportunity to characterize changes along environmental gradients (Poff et al. 2006). The pioneering paper by Webb et al. (2002) propelled the analysis of community composition to a new flourishing research framework of phylogenetic community ecology, incorporating evolutionary history of traits and phylogenetic relationships between species to provide insights into the importance of ecological process in shaping community structure.

It is now undeniable that humans have had an impact on the environment at the planetary scale. The term Anthropocene has appeared in more than 500 peer-reviewed articles. Even though there is ongoing debate as to whether we have crossed the boundary from the Holocene to the Anthropocene (Ruddiman et al. 2015), understanding the basic principles of community ecology, diversity and composition across different temporal and spatial scales is increasingly important to predict new combinations of species and environments, functioning of ecosystems, and the benefits and problems of these changes to society (Jackson and Blois 2015).

1.2. LITERATURE REVIEW

1.2.1. CONCEPTS

1.2.1.1. Community analysis

Whittaker (1972) separated biodiversity into two spatial components: alpha-diversity (within site distribution of species) and beta-diversity (between site species variation). A large array of quantitative diversity measures exists (e.g. Hill 1973, Gotelli and Colwell 2001, Magurran 2004), which makes it a challenge for ecologists to choose the appropriate measures (Fiedler and Truxa 2012). Using only taxonomic identity to understand community assembly rules limits understanding of biological mechanisms to environmental constraints (Larsen and Ormerod 2010). The species traits (functional structure), phylogenetic relationships, landscape structure, and spatial scales may help us understand the ecological and evolutionary factors that determine community assembly. Few studies have investigated patterns of diversity that consider a few of these approaches simultaneously (e.g. traits and phylogeny: Cavender-Bares 2006, Vamosi and Vamosi 2007; phylogeny and environment: Horner-Devine and Bohannan 2006; traits, scale and environment: Arnan *et al.* 2012).

1.2.1.2. Phylogenetic structure

Several recent studies have analyzed phylogenetic community structure under two models driven by different processes: niche-related and neutral models. Niche-based models assume that deterministic mechanisms affect community composition. Several types of processes can influence phylogenetic community structure: competition, environmental filtering (Webb 2000, Cavender-Bares *et al.* 2006), facilitation and dispersal (Emerson and Gillespie 2008). These general processes can create phylogenetic overdispersion or clustering of co-occurring species. Past or current competition tends to keep closely related species from co-occurring (Lovette & Hochachka 2006) while environmental filters constrain certain species traits that are important for their persistence in a particular environment (Cavender-Bares *et al.* 2004, Horner-Devine and Bohannan 2006) by attracting closely related species with conserved traits, or distantly related species that have converged on similar niche use (convergent traits) (Webb *et al.* 2002). On the other hand, neutral models proposed by Bell (2000) and Hubbell (2001) are driven by stochastic processes including birth, death, dispersal, and speciation rates. This model differentiates between local and regional communities, and makes the assumption that all species are ecologically equivalent in a community and that specialization and interaction between species and the environment play no role in explaining biodiversity patterns. This implies that

biodiversity and extinction arise at random. The neutral model is often considered as a null hypothesis to the niche theory (Nee and Stone 2003, Harte 2004). Several studies have been conducted in a wide variety of ecosystems to test the predictions of those models; however, studies have supported either the niche model (Fine and Kembel 2011, Hennequin et al. 2014), neutral model (Smith 2015, Silvertown et al. 2006) or were intermediate between the two (Cardillo 2011, Chalmandrier et al. 2015, Elliott et al. 2016). Efforts are being made to unify those models into a more general explanation for the processes controlling community dynamics (Tilman 2004, Gravel et al. 2006).

1.2.1.3. Functional traits

Integrating functional traits with phylogenetic relatedness can provide additional information about the role of isolation and speciation in driving biodiversity patterns in different environments (Graham and Fine 2008). The relationship between phenotype evolution and phylogenetic distances is known as phylogenetic signal. Trait convergence or conservation will influence the phylogenetic structure of a local community depending if environmental filtering or competition is the driving process (Pausas and Verdú 2010). Conserved traits are passed from common ancestors to descendants and are common between descendants, while convergent traits are shared by distantly related species. Functional traits dominant in a community reveal adaptive values to environmental gradients and the importance of niche-related processes in structuring communities. If no functional trait patterns are found, neutral processes are probably acting or the traits measured do not have an adaptive value (Hoiss et al. 2012). Incorporating functional traits in a study can improve the explanatory power of the response to different processes, such as fragmentation, habitat loss, or climate change (Öckinger et al. 2010).

1.2.1.4. Landscape structure

MacArthur and Wilson's (1967) conceptual theory of island biogeography proposed interactions between immigration and extinction as the main forces responsible for species richness on islands. Their hypothesis predicts that species richness varies positively with increasing island area and negatively with increasing distance from the source of colonists. This model has also been applied in interpretation of diversity patterns in heterogeneous and fragmented landscapes in terrestrial habitats. Assuming that the matrix separating habitat patches does not influence

species abundance and composition, it is predicted that small isolated patches should have lower species richness than large or near species source patches due to a higher rate of immigration and higher number of microhabitats. However, there is an increasing recognition that the surrounding matrix can influence species abundance and composition in fragmented habitats (e.g. Diamond 1975, Gilpin and Hanski 1991, Wilson 1992, Cook et al. 2002, Öckinger et al. 2012).

Species patterns and processes are affected by different mechanisms, from the mosaic of their habitat land cover types to the composition of the land cover surrounding their habitats. This matrix of surrounding heterogeneous habitats may drive colonization-extinction dynamics by limiting dispersal (e.g. Ricketts 2001, Revilla et al. 2004), by modifying resource availability (Grundel and Pavlovic 2007) and by increasing edge effects (Saunders et al. 1991). The impact of the landscape matrix may be different depending on anthropogenic disturbance, amount and configuration of natural patches (Kennedy et al. 2010). Moreover, communities occur on gradients of environmental variables and these interactions (e.g. facilitation, predation, and competition) along with species functional traits may determine community structure (Davis et al. 1998, McGill et al. 2006).

1.2.1.5. Scales

Numerous studies have demonstrated that the scale at which we sample has consequences on the processes found that structure ecological assemblages (Cavender-Bares 2006, Ellwood et al. 2009, Cardillo 2011, Chase and Myers 2011), because the metacommunity is a set of local communities that are linked by dispersal events of potentially interacting species (Leibold et al. 2004). To develop successful conservation strategies to stop the loss of biodiversity we need to understand the factors affecting species richness and composition. As ecological processes affect species diversity patterns on different spatial scales (Willis and Wittaker 2002, Tschardt et al. 2012), it is necessary to investigate the effect of species-species and species-habitat interactions on a local scale as well as dispersal limitation and surrounding matrix composition on a landscape scale. Phylogenetic scale (taxonomic groups or subsets) has also been shown to influence the patterns observed in phylogenetic structure (Silvertown et al. 2001, Cavender-Bares 2006).

1.2.2. STUDY HABITATS AND ORGANISMS

1.2.2.1. Wetlands in Canada

Wetlands occupy about 14% of Canada's surface. Human disturbances have significantly altered the roles of wetlands in improving water quality, protecting shorelines, stabilizing water supplies, moderating the effects of floods, and recharging groundwater aquifers (Keiper et al. 2002, Calmé et al. 2002, Dubé et al. 2011, Pasquet et al. 2014). The key anthropogenic stressors of wetlands are agriculture, industrial/urban development and contamination, climate change, and non-native invasive species. Currently in Canada, more than 60% of wetlands have been transformed (Environment Canada 1993). Conservation of biodiversity is growing in interest and wetlands are disappearing at an alarming rate, so understanding how communities assemble and how interactions among species and ecosystems influence ecology and evolution is critical. Thus these habitats can be used as a model to investigate the role of a landscape matrix that has undergone historic area loss and fragmentation. This gives an opportunity to explore the influence of matrix land cover on species functional traits and phylogenetic relationships.

Wetlands are ecosystems saturated in water within 30 cm of the soil surface or inundated long enough (two weeks or more) to modify the substrate, creating anaerobic conditions and characteristic vegetation composition. Vegetation is adapted to a wet environment and organic or mineral soils (National Research Council 1995, National Wetlands Working Group 1997). Approximately 25% (1 270 000 km²) of the world's wetlands are in Canada (Dahl and Zoltai 1997). The Canadian Wetland Classification System separates wetlands into five classes: marsh, swamp, bog, fen and shallow water (National Wetlands Working Group 1997). The classification is based on vegetation, hydrology, origin of water, soil type, landform and local climate. Canadian wetlands are concentrated between 45° and 75° N. Their distribution depends on climate, landforms and the physical and chemical composition of the soil surface (National Wetlands Working Group 1997).

Bogs are nutrient poor, low in calcium and magnesium, and peat covered wetlands with acidic water between pH 4.0 and 4.8 (Gorham and Janssens 1992). Rainfall is the only source of water and nutrient intake (ombrotrophic). The water table is at or slightly below the surface and the peat layer is 40 cm or more in thickness (National Wetlands Working Group 1997). Vegetation is

dominated by *Sphagnum*, other mosses, ericaceous shrubs, and cotton grass (Cyperaceae) (Payette 2001).

Fens are peatlands with a highly fluctuating water table, high organic matter and nutrient rich minerotrophic waters. The dominant source of water comes from groundwater, which is generally associated with high pH and high levels of nutrients (Kolka and Thompson 2006). Fen soils are generally higher in mineral content and oxygen saturation than in bogs (National Wetlands Working Group 1997) and the peat layer is composed of decomposed sedges and brown mosses. Vegetation composition is related to the water table level and the water chemistry which separate fens into two types: rich (pH 5.5 to more than 6.9) and poor (pH of 4.5 to 5.5). Vegetation is dominated by sedges, grasses, reeds, bryophytes (mostly brown mosses), some shrubs and sparse tree cover (Tiner 1999).

Marshes are characterized by mineral soils high in organic matter that are periodically inundated by standing or slow moving nutrient-rich water. Vegetation is usually composed of aquatic macrophytes, rushes, reeds, grasses, sedges, shrubs, brown mosses, macroscopic algae and other herbaceous plants. Water sources include stream inflow, precipitation, groundwater discharges and tidal action. The accumulation of aquatic plant material and peat is low. Marshes tend to be circumneutral or alkaline due to the presence of dissolved minerals (National Wetlands Working Group 1997).

Swamps are characterized by mineral or organic soils rich in nutrients dominated by woody plants such as trees and shrubs. The peat is primarily decomposed woody debris. The water table is below or at the ground surface which allows trees and tall shrubs to grow and cover more than 30% of the surface. The nutrient content is very variable which leads to acidic or basic pH (National Wetlands Working Group 1997).

Shallow waters are standing water transitional between permanent waters, such as lakes, and the other four types of wetlands. Open water covers more than 75 % and is less than 2 m deep, the remaining is covered by emergent vegetation. The soil below water is mineral or organic. (National Wetlands Working Group 1997).

1.2.2.2. Arthropods in wetlands and variation with spatial scales

The arthropod communities in these threatened habitats have been poorly documented, even though it has long been suggested that wetland restoration success should be based on more than vegetation (Zedler 1993). A study in Alberta (Finnamore 1994) found that arthropods represent 77% of all species in a boreal fen compared to 16% for plants and 6% for vertebrates. Arthropods, especially insects, have a significant impact on ecosystem processes, because they occupy an array of niches and play many different functional roles. With their high variety of feeding habits, high reproductive capacity, and short generation time they are resilient to environmental changes (Kim 1993). Wetland insect inhabitants are often adapted to specific conditions, and can be obligatory associates or characteristic of a wetland class (Spitzer and Danks 2006). Thus, it is critical to understand the community structure of insects if we are to understand the biodiversity and functioning of wetlands.

Understanding patterns of species diversity at different spatial scales is also critical for management and conservation of wetlands. Perović et al. (2015) recommended that to maintain high taxonomic and functional diversity of butterfly communities in managed grasslands, promoting high landscape compositional heterogeneity was outweighing the effects of local land-use intensity by supporting a larger species pool. Rubene et al. (2015) showed that the diversity of wild bees and wasps in managed forests was locally affected by flowering plants and the state of the sites (burned vs unburned) supporting similar species richness, but different species composition. Surrounding landscape composition and area also had an effect on species richness. Different species pools colonizing the different landscapes within regions were explaining the high species turnover between landscapes on a scale of 10-100 km². These communities are composed of different ecological groups affected by different habitat characteristics. Decler et al. (2015) showed that species richness at the local scale of wetland inhabiting spiders, long-legged flies and ground beetles was primarily affected by landscape factors such as density of ditches acting as corridors and wetland area. On the other hand, species composition was mainly determined by the site type.

1.2.2.3. Ecological diversity of wetland Diptera

Species richness and abundance of Diptera can be high in wetlands (Beaulieu and Wheeler 2005; Grégoire Taillefer and Wheeler 2010; Keiper et al. 2002). The families Empididae (Barták and Roháček 1999), Dolichopodidae (Pollet 1992, Rampazzi 2002), Chironomidae (Wrubleski 1987), Sphaeroceridae (Marshall 1994), Chloropidae (Grégoire Taillefer and Wheeler 2011), several other acalyptrate families (Roháček and Máca 1982, Roháček *et al.* 1998) and biting flies (Lewis 1987) have been inventoried from a variety of peatlands around the world. Blades and Marshall (1994) surveyed the terrestrial arthropod fauna associated with the substrate (based on pan trap collections) of southern Ontario peatlands and found 50 families of Diptera, representing 522 species. Beaulieu and Wheeler (2001) identified 338 Brachycera species in *Carex* meadows in southwestern Quebec. Savage et al. (2011) collected 6700 specimens and 381 species in six ombrotrophic bogs in temperate southern Quebec and Vermont. In one of our previous studies of Diptera in Quebec peatlands, 427 species and more than 12,800 specimens were collected in three natural bogs (Grégoire Taillefer and Wheeler 2012). The most species rich families of higher flies were, in decreasing order: Sphaeroceridae, Dolichopodidae, Tachinidae, Sarcophagidae, Empididae, Syrphidae, Chloropidae, and Ephydriidae.

1.2.2.4. Diptera phylogenetic relationships

Diptera includes more than 10% of all described animal species, having an estimated 150,000 described species (Pape and Thompson 2010). Diptera is one of the most species-rich, ecologically diverse of the four megadiverse insect orders: Diptera, Coleoptera, Lepidoptera and Hymenoptera (Kitching et al. 2005). The dipterist Willi Hennig, developed methodological tools and precise phylogenetic concepts, which led to repeatable and more objective approaches to classify Diptera. He first started by establishing the higher level phylogenetic relationships of lower Diptera and Cyclorrhapha (Hennig 1954–1971), then phylogenetically classified the entire order (Hennig 1973). Recent research has continued to test Diptera phylogenetic relationships using morphological and molecular data with more sophisticated and consistent methods of analyses at higher levels (e.g. Yeates and Wiegmann 1999, Wiegmann et al. 2011, Lambkin et al. 2013) as well as species and genus level phylogenies for some families (e.g. Brake 2000, Beckenbach and Borkent 2003). There is strong molecular support for the monophyly and limits of Diptera (Yeates and Wiegmann 1999, Wiegmann et al. 2011); there are also several

morphological synapomorphies, some of the most obvious of which are the modification of the mouthparts and reduction of the hind wings into halteres (Hennig 1973). Early diversification of Diptera suborders probably occurred in the Triassic as fossil diversity increased during the Jurassic (Kovalev 1979, Woodley 1989); however, there is no fossil record of many higher Diptera groups for this period.

Diptera are separated into two major sub-orders: Lower Diptera and Brachycera. Within Brachycera, the clade Schizophora contains more than 80 families, and 60 families in the Nearctic region of the 150 families of Diptera that are recognized (McAlpine et al. 1981, McAlpine 1989, Yeates and Wiegmann 1999). They are diverse not only in species number but in their feeding habits, ecology, morphology and body size. Schizophora includes the familiar house flies, fruit flies and relatives. Schizophora fossils are known mostly from Cenozoic amber deposits; consequently, the origins of Schizophora may be more recent than other major Diptera groups, likely in the Cretaceous between 65 and 135 MYR ago (Beverley and Wilson 1984, Grimaldi and Cumming 1999), and their major diversification probably occurred rapidly in the early Cenozoic (Wiegmann et al. 2011).

Although the phylogenetic relationships of lower Diptera are known with strong quantitative support (Collins and Wiegmann 2002), the phylogenetic relationships within Schizophora have remained poorly resolved until recently (Junqueira et al. 2016). This is mostly due to high species diversity, extremely rapid diversification in the early Cenozoic, a lack of fossils during critical time periods, and disagreement between morphological and molecular characters (Wiegmann et al. 2011). Junqueira et al. (2016) have used complete mitochondrial

Schizophora contains two groups, each comprising several families, the Calyptratae and Acalyptratae. Schizophora and Calyptratae are recognized as monophyletic groups by morphological (Hennig 1972, 1973, Yeates et al. 2007, Lambkin et al. 2013) and molecular data sets (Lessinger et al. 2000, Junqueira et al. 2004). The monophyly of the Acalyptratae still remains uncertain. Wiegmann et al. (2011) supported non-monophyly of acalyptrates. However, large gaps remain. The molecular study by Han and Ro (2005) is one of the phylogenetic analyses with extensive Schizophora family and species coverage, representing 18 families and

47 species.

The availability of molecular sequence data for Diptera is fragmentary because of a focus on economically and medically important species (Junqueira et al. 2004). Junqueira et al. (2016) have used complete mitochondrial genomes to resolve Schizophora radiation and estimate divergence times. They also found that a monophyletic Calyptrate clade was nested inside a paraphyletic Acalyptratae section. Despite the rapid and extensive diversification of Schizophora, their taxonomy and phylogeny have been poorly studied, especially at taxonomic levels below that of family. For meaningful progress in community phylogenetic research on Diptera, it is critical to address major gaps in the taxonomy and phylogeny of Schizophora, even in regions that are considered well-known, such as temperate Canada. For this reason, any analysis of community ecology of Canadian wetland Diptera in a phylogenetic context requires fundamental research in taxonomy and phylogeny reconstruction before quantitative analyses are feasible. This gap in taxonomic and phylogenetic resolution makes Diptera a more challenging group for ecological study than more well-known taxa such as vertebrates or most plants. Recent progress in the use of DNA barcodes has led to significant growth in available data on species richness of Canadian Diptera (e.g. Hebert et al. 2016), but we still lack basic taxonomic resolution, species names and information on phylogenetic relationships at the species level.

This thesis will investigate patterns of diversification within Schizophora present in Quebec wetlands. Historical processes of diversification using divergence time estimates between species and geographical populations will be investigated using mitochondrial gene sequence data. Several taxa present in Quebec wetlands were previously unrepresented in GenBank or BOLD, and even species present in those databases are often unidentified to the genus or species level. Thus, a combination of available sequences from GenBank and BOLD, along with newly sequenced specimens from wetland sampling, is necessary to provide sufficient taxonomic and genetic resolution to clarify unresolved phylogenetic relationships, and thus community structure among wetland Schizophora.

1.3. OBJECTIVES

The aim of this thesis is four-fold: 1) Compare diversity and species assemblages of Diptera

within and between three types of wetlands (bog, marshland, swamp) and in bogs only at a larger spatial scale; 2) determine if the functional and phylogenetic structure of Diptera communities is clustered, overdispersed or random and whether the structure differs with spatial scale; 3) Determine if functional traits and/or environmental characteristics (isolation, latitude, climate, size, surrounding matrix, local characteristics) influence Diptera community structure and at which spatial scale; 4) Evaluate the variation of relatedness along environmental and spatial gradients.

1.4. HYPOTHESES AND PREDICTIONS

In order to meet these objectives, I tested the following hypotheses:

Hypothesis 1: Species assemblages will be different between all sites, but the differences will be more pronounced between than within ecoregions and between than within wetland types. Diversity will increase from northern to southern peatlands.

Hypothesis 2: Community assembly will fluctuate in a deterministic way. If ecologically important traits are conserved, coexisting species at the local scale (trap) will exhibit more phylogenetic overdispersion. This is because at small spatial scales competition and density-dependent mechanisms are more important, which prevent similar species from co-occurring. Clustering will increase with increasing spatial scales, because of greater environmental heterogeneity, so species with similar traits can sort across more habitats and related species tend to be concentrated in the region in which they originated. Habitat filtering will be more important than competition in the three wetland types, as only certain species possess adaptations to survive. The most stressful habitat, bogs, will act as a stronger ecological filter than the less stressful swamp habitat.

Hypothesis 3: Diversity and community composition at the local scale will be related to local characteristics such as plant diversity, soil composition and certain species traits or trait combinations. At the landscape and regional scale, diversity and community composition will be associated with landscape characteristics such as community isolation, latitude, wetland size and the surrounding matrix which will influence dispersal and species turnover. Beta diversity will be related to barriers to dispersal such as distances between sites and urban development.

Hypothesis 4: Diversity, phylogenetic and functional relatedness will vary along some important environmental variables, such as vegetation composition and pH (from poorer ombrotrophic bog to richer minerotrophic swamp habitats) as well as geographical space such as latitude and degree of urbanization.

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1.6. CONNECTING STATEMENT

The introduction and literature review in Chapter 1 provide the context for the research projects in the following two Chapters. In Chapter 2, I compare the diversity and community composition of Diptera in three types of wetlands in the Montreal Metropolitan Area and surroundings, Quebec. I use three approaches to measuring biodiversity: taxonomic identity, functional trait diversity, and phylogenetic relationships and explore which environmental variables are responsible for the patterns observed. Chapter 3 uses a similar procedure although I describe patterns at different spatial scales in bogs in three Quebec ecoregions.

CHAPTER 2: Effect of habitat type on taxonomic, phylogenetic and functional diversity of wetland Diptera

2.1. ABSTRACT

Different processes drive spatial variation in community composition. Standard measures of composition are useful in species-based conservation and ecology, but they may be less informative in the context of evolutionary history and functional diversity. Phylogenetic approaches are increasingly used to test deterministic and stochastic hypotheses of community assembly. Species traits can be integrated with phylogenetic relatedness to provide additional information about mechanisms driving biodiversity patterns. We studied 28 families of flies (Diptera) with a range of functional characteristics in three wetland classes (bogs, swamps, marshes) near Montreal, Quebec, Canada. We examined taxonomic, phylogenetic and functional structure of Diptera communities and assessed if rarity is deterministic or essentially stochastic. We also examined how beta- and phylobeta-diversity are related to local environmental conditions, patch area, and/or surrounding landscape. Phylogenetic community structure analyses had high value and complementarity to standard measures. Environmental filtering acted on bog communities during assembly, as they emerged from a slow peat accumulation process and the plant composition is characteristic as few species can survive in these acidic and low nutrient conditions. Subsequently, community assembly happened randomly. Neutral processes of community assembly are more important in marshes and swamps, as dispersal limitation explained species abundance dynamics of small and common Diptera species within habitat type. The assembly of marsh Diptera communities is a balance between neutral processes and environmental filtering, while assembly in swamps can be seen as neutral. Clustering increased with environmental extremes, indicating environmental filtering. Rare species tended to be less closely related to common species. They have unique habitat requirements and the high diversity is maintained by temporal turnover of species with similar traits filtered by the environment.

Keywords

Phylogenetic structure, rare species, community assembly, environmental factors, functional structure, neutral processes, environmental filtering

2.2. INTRODUCTION

What are the processes underlying spatial variation in species richness and community composition? Standard measures of species richness and composition (e.g. Gotelli & Colwell 2001, Magurran 2004) focus mainly on alpha and beta diversity. Although these metrics are important in conservation and ecology, they can be uninformative in the context of evolutionary history and functional diversity, as they treat all species as ecologically equivalent and evolutionary independent (Swenson et al. 2012). A promising complementary modern approach has been built on the incorporation of phylogenetic data in ecological analyses (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2009).

Several recent studies have analyzed phylogenetic community structure under two models driven by different processes: niche-related and neutral models. Niche-based models assume that deterministic mechanisms affect community composition. Several types of processes can influence phylogenetic community structure: competition, environmental filtering (Webb 2000, Cavender-Bares et al. 2006), facilitation and dispersal (Emerson and Gillepsie 2008). These general processes can create phylogenetic overdispersion or clustering of co-occurring species. Past or current competition tends to keep closely related species from co-occurring (Lovette and Hochachka 2006) while environmental filters constrain certain species traits that are important for their persistence in a particular environment (Cavender-Bares et al. 2004, Horner-Devine and Bohannan 2006) by phenotypically attracting closely related species (conserved traits) or distantly related species that have converged on similar niche use (convergent traits) (Webb et al. 2002). On the other hand, neutral models (Bell 2000, Hubbell 2001) are driven by stochastic processes including birth, death, dispersal and speciation rates. This model differentiates between local and regional communities, and makes the assumption that all species in a community are ecologically equivalent and that specialization and interaction between species and the environment play no role in explaining biodiversity patterns. This implies that biodiversity and extinction arise at random. This model is often considered as a null hypothesis to niche theory (Nee and Stone 2003, Harte 2004,). Several studies have been conducted in a wide variety of ecosystems to test the predictions of these models; however, results vary widely with assemblages either clustered (Fine and Kembel 2011), overdispersed (Hennequin et al. 2014), or random (Smith 2015) or an amalgamation between the three depending on spatial and taxonomic

scales (Cardillo 2011, Chalmandrier et al. 2015, Elliott et al. 2016). Efforts have been made to unify these models into a general explanation for the processes controlling community dynamics (Tilman 2004, Gravel et al. 2006).

Integrating species traits with phylogenetic relatedness across space will provide additional information about the role of isolation and speciation in driving biodiversity patterns in different environments (Graham et al. 2008). The relationship between phenotypic evolution and phylogenetic distances between species gives a phylogenetic signal. Trait convergence or conservatism will influence the phylogenetic structure depending on whether environmental filtering or competition is the driving process (Pausas and Verdú 2010). Functional traits dominant in a community reveal adaptive values to environmental gradients and the importance of niche-related processes in structuring communities. If no functional trait patterns are found, neutral processes are probably acting, or the traits measured do not have an adaptive value (Hoiss et al. 2012). Incorporating traits in a study can improve the explanatory power of the response found for different processes, such as fragmentation, habitat loss, or biodiversity (Öckinger et al. 2010).

Species patterns and processes are affected by different mechanisms from the mosaic of their habitat types to the composition of the land cover surrounding their habitats. This matrix of surrounding heterogeneous habitats may drive colonization-extinction dynamics by limiting dispersal (e.g. Ricketts 2001, Revilla et al. 2004), by modifying resource availability (Grundel and Pavlovic 2007) and by increasing edge effects (Saunders et al. 1991). The impact of the landscape matrix may be different depending on anthropogenic disturbance, amount and configuration of natural patches (Kennedy et al. 2010). Moreover, communities occur on gradients of environmental variables and these interactions (e.g. facilitation, predation, and competition) along with evolutionary relationships and species functional traits may determine community structure (Davis et al. 1998, McGill et al. 2006). However, the role of functional and phylogenetic diversity in organizing species distribution across different environments has not been studied extensively and further studies are needed to determine the interactions between rarity, taxonomic and/or phylogenetic diversity and structure (Vamosi and Vamosi 2007).

Conservation of biodiversity is becoming a high priority in threatened and vulnerable habitats such as wetlands, so understanding how communities are assembled and how interactions among species and ecosystems influence evolution is critical to management of these habitats (Cavender-Bares et al. 2009). To conserve, manage, and restore wetland biota, we need to understand what is influencing the dynamics of communities, their diversity, and ecosystem function. Wetlands are one of Canada's most characteristic and recognizable habitats. Canada's wetlands comprise an estimated 24% of the world's wetlands and are important ecologically as habitats, nutrient and carbon sinks, water supplies, etc. Wetlands have been lost, fragmented, and drained for horticultural peat mining, forestry, urbanization and agriculture (Lavoie and Rochefort 1996, Waddington and Price 2000). Most of the loss has taken place near urban areas, where access is easy.

We studied several Diptera families covering a broad range of functional characteristics in three classes of wetlands (bogs, marshes, swamps) in the Montreal metropolitan area and surroundings, Quebec, Canada. Bogs are peat-covered wetlands, low in nutrients and acidic with pH between 3 and 5. They have characteristic vegetation dominated by *Sphagnum* mosses (Gorham and Janssens 1992, Payette 2001). Marshes are rich in nutrients as they are periodically inundated. They contain shallow water, 15 to 90 cm in depth with pH > 5, which allows emergent herbaceous vegetation to grow. Swamps are dominated by trees and shrubs where the water at or below the surface is rich in nutrients and usually neutral with pH around 7.2 (National Wetlands Working Group 1997). This study characterized the diversity, distribution, ecological roles, and conservation status of Diptera present in wetlands isolated in an anthropogenic matrix, and assessed the mechanisms that structure community phylogenetics and beta diversity.

We examined whether 1) wetland Diptera communities exhibit taxonomic, phenotypic, and phylogenetic structure and 2) whether rare species within wetland habitats are ecologically dissimilar to common species or whether commonness and rarity are essentially stochastic. Also, we examined 3) how taxonomic, phylogenetic, and functional compositions are related to local environmental conditions, patch area, and/or surrounding landscape. We hypothesized that species composition is related to local conditions and diversity follows a gradient from poorer (ombrotrophic) to richer (minerotrophic) habitats, specifically bogs to marshes to swamps.

Habitat filtering is more important than competition in these harsh habitats, as only certain species possess the necessary adaptations. The most stressful habitat, bogs, act as a stronger ecological filter than the less stressful swamp habitat. Beta diversity is related to dispersal barriers such as distance between sites and urban development.

2.3. MATERIALS AND METHODS

Four wetlands in each class were sampled for Diptera in summer 2013 (Fig. 2.1). Wetlands were classified following the Canadian Wetland Classification System (National Wetland Working Group 1997). Wetlands were chosen from high resolution digital aerial photos available from Ducks Unlimited Canada for the territory of the Montreal metropolitan area (Beaulieu et al. 2010) and from personal communication with experts. To standardize the wetland type, open raised bogs with pH < 4.5 dominated by *Sphagnum* mosses, ericaceous shrubs and a tree cover of less than 30% were chosen. Marshes were covered with permanent shallow water with pH between 5.5 and 7.4. Swamps were covered entirely by deciduous trees and the water table was at the ground surface at the beginning of the season. Sampling was conducted weekly for six weeks in the period of highest species richness and activity from 8 July 2013 to 11 August 2013 with pan traps and sweeping on an area of 30 m x 30 m in the centre of each wetland if accessible. Sweep samples were collected on three transects of 20 m in each site. The location of sweep transects within each site differed from week to week. Three transects of four pan traps were placed 10 m apart on a 30 m transect in the center of each site and emptied every 7-8 days. Traps consisted of yellow plastic bowls (4.5 cm deep and 12.5 cm diameter) placed in the soil with their upper rim flush with the ground surface and filled with a 50% solution of propylene glycol and water, with a drop of liquid detergent as a wetting agent.

Insects were preserved in 95% ethanol for subsequent DNA extraction. Small flies were dried using hexamethyldisilazane; larger flies were transferred into ethyl acetate, then pinned and air-dried. Specimens were deposited in the Lyman Entomological Museum (McGill University, Ste-Anne-de-Bellevue, QC). All specimens of higher Diptera (Schizophora) were identified to named species, if published taxonomic keys or taxonomic expertise was available, or to numbered morphospecies.

The definition of rarity used in this study is based on three indirect rarity measures: 1- Restriction to a wetland habitat (restricted: found in only one wetland type; intermediate: found in two wetland types; broad: found in three wetland types); 2- Frequency of occurrence (rare: only found in one site; infrequent: found in 2 to 5 sites; intermediate: found in 6 to 9 sites; widespread: found in 10 to 12 sites) and 3- Number of specimens collected (rare: $< 0.6\%$ of total catch; common : $\geq 0.6\%$ of catch). To separate rare and common species, an inflection point criterion was used. The rank abundance curve for the total abundance was examined and the inflection point was where the curvature changed (Siqueira et al. 2012). Each species was also assign to a category in seven biological traits: larval feeding habit, specialization to wetlands, size, generalist/specialist, voltinism, overwintering forms, and habitat preference for oviposition (Appendix 2.1).

Water pH, conductivity and soil temperature measurements were taken with Hanna pocket EC/TDS and pH Tester at two locations in the 30 x 30 m area in each site in week one. Fluctuation of water-table depth over the season was estimated visually with the PVC tape discolouration method (Belyea 1999). The following ground cover attributes were surveyed in five 1 m x 1 m quadrats placed at each corner and in the middle of the 30 m x 30 m area: percent plant species cover, litter cover, canopy cover, and open water cover. Landscape composition and wetland area were measured using the Earth Observation for Sustainable Development of Forests land cover datasets of circa year 2000 at a spatial resolution of 25 m (Wulder et al. 2008) and QuantumGIS version 1.8.0 (QGIS 2012). Open water, exposed land, urban development, low vegetation, wetland, forest and agriculture surrounding each wetland were measured within a circle with a 2 km radius because Diptera have been found to respond to the surrounding matrix at this spatial scale (Meats and Smallridge 2007, Savage et al. 2011) (Appendix 2.2).

2.4. STATISTICAL ANALYSES

2.4.1. Diptera diversity and community structure

Diptera communities in each site were characterized by relative abundance, observed species richness and diversity from samples of pan traps and sweeping pooled by week and throughout the season. Diversity was assessed with rarefaction curves based on 1000 permutations with species richness as a diversity index using the vegan package (Oksanen et al. 2015) in R version

3.2.2 (R Core Team 2015). Significance of differences in overall relative abundance, observed species richness and rarefied species richness among wetland type were determined based on ANOVA F tests.

The habitat association of each species was examined using indicator species analysis performed with the function *multipatt* in the package *indicspecies* (De Cáceres and Legendre 2009). The association of each species with individual or combinations of classes in each wetland type was applied. The significance of species association was assessed with a permutation test using 999 permutations. Only species with ≥ 10 individuals and an indicator value (IndVal) $\geq 85\%$ were considered.

A Non Metric Multidimensional scaling (NMDS) ordination was used to assess differences among sites and weeks in relation to their Diptera community composition using the function *metaMDS* of the *vegan* package. A Hellinger transformation (Legendre and Gallagher 2001) was used on the species data to give low weight to rare species. A Permutational Multivariate Analysis of Variance based on a Bray-Curtis distance matrix was used to assess significance of differences among habitats using the function *Adonis* of the *vegan* package. Ground cover variables were reduced with principal component analysis (PCA) using the correlation matrix (Dormann et al. 2013) and principal components (PC) were used in subsequent analyses. Significant PCs were identified using the Kaiser-Guttman criterion (Yeomans and Golder 1982). Variables with loadings larger than 0.32 were forming the clusters of interest (Booth et al. 1994) (Table 2.1). Latitude and longitude were transformed into the corresponding coordinates in X (east-west) and Y (north-south) distances using the function *geoXY* in the package *SoDA* (Chambers 2008). To reduce the number of environmental variables in the subsequent analyses and to avoid autocorrelation between them, first all remaining environmental variables were observed with scatterplots and Pearson's correlation indices were calculated for all combination of variables (Skidmore et al. 2013). The resultant matrix included the PC1 to 4, X and Y coordinates, % tree cover, % water above surface, conductivity, plant richness and all landscape variables. Environmental variables were standardized prior to subsequent analyses. The function *envfit* of the *vegan* package was used to examine the significant relationships between the environmental variables and species occurrence, using 999 permutations.

2.4.2. Phylogeny reconstruction

Due to a lack of resolved phylogeny for Brachycera (Diptera), a dated tree of Brachycera was generated with paleontological calibration dates. A single gene tree was used as a proxy for a species tree (Joly et al. 2014). Sequences of the 658 bp fragment of the cytochrome *c* oxidase subunit I (COI-5P) gene of Eremoneura, Cyclorrhapha and Schizophora taxa for this phylogeny were obtained from the Barcode of Life Database (BOLD) (Ratnasingham and Hebert 2007) or from our own sequenced specimens. 356 specimens of 139 species not available in BOLD were sent for DNA barcoding at the Canadian Centre for DNA Barcoding, Guelph, Ontario using *C_LepFolF/C_LepFolR* primer sets (Hernández-Triana et al. 2014). Sequences of *Dolichopus brevipennis* (Dolichopodidae), *Sphaerophoria philanthus* (Syrphidae), *Chelipoda truncata* (Empididae), *Hypocera ehrmanni* (Phoridae), and *Lonchoptera furcata* (Lonchopteridae) were used to root the tree (outgroup). Monophyly was constrained for families, sub-families, genera and groups in which there were recent and well-supported, multi-gene or morphological phylogenies for Schizophora: selected Acalypratae groups (Yeates and Wiegmann 2005); Schizophora and Calypratae (Lambkin et al. 2013); Sarcophagidae (Kutty et al. 2010, Pape et al. 2011); *Ravinia* (Sarcophagidae) (Giroux et al. 2010, Piwczynski et al. 2014); *Boettcheria* (Sarcophagidae) (Piwczynski et al. 2014); Luciliinae and Polleniinae (Calliphoridae) (Kutty et al. 2010); Phytomyzinae (Agromyzidae) (Scheffer et al. 2007); Scathophagidae (Bernasconi et al. 2000); Milichiidae (Brake 2000); Sciomyzidae, Sciomyzini, Tetanocerini (Tóthová et al. 2013); Tephritidae (Han and Ro 2009); Drosophilidae (Yassin 2013); Chloropinae (Chloropidae): Brake 2000).

A Bayesian approach was used for phylogenetic analyses because it allows for both phylogenetic relationship assessments and divergence time estimates for speciation rates (Espíndola et al. 2012). Trees were generated with the program BEAST v1.7.5 (Drummond et al. 2012) and the output was examined via Tracer v.1.6 (Rambaut et al. 2014). The MUSCLE (Edgar 2004) multiple alignment software was used to produce an aligned data matrix. Because no suitable calibration points or mutation rates for the study taxa exist, we used JModelTest2 (Guindon and Gascuel 2003, Darriba et al. 2012) and Akaike Information Criterion to determine which model of nucleotide substitution best-fit the alignment. This gene-based quantitative analysis was

chosen with a fossil-based analysis because the fossil record is very limited.

In all analyses, strong priors were set on the age of two nodes corresponding to Schizophora (LogNormal: Mean = 3, St. Dev. = 0.78, offset = 70) and Chloropidae (LogNormal: Mean = 3, St. Dev. = 0.7, offset = 42) according to paleontological and molecular data (Nardi et al. 2010, Wiegmann et al. 201). The appropriate model selected by JModelTest2 was GTR+I+G and no partitioning by codon was used. A branching prior was set under a Yule process model and a relaxed molecular clock was assumed using a LogNormal distribution of rates (Drummond et al. 2006). The analysis was performed twice for a MCMC chain length of 40 million generations (10000 echo states, 4000 log parameters, 10% burn-in) (Figure 2.2).

2.4.3 Phylogenetic and functional community structure

Phylogenetic signal for categorical traits were measured using the *fitDiscrete* function in the package Geiger (Harmon et al. 2008). Pagel's lambda was used as a tree transformation that assesses the degree of phylogenetic signal within the trait. Maximum likelihood estimates of lambda were compared with a model with no phylogenetic signal where the tree topology was transformed to one giant basal polytomy that has all internal branch lengths multiplied by 0 (i.e. $\lambda = 0$) (Freckleton et al. 2002). Significance of the models was assessed by comparing them with a chi-square distribution. For the continuous trait (size) the K statistic (Blomberg et al. 2003) in the package picante (Kembel et al. 2010), that compares the observed signal in a trait to the signal under a Brownian motion model of trait evolution on a phylogeny, was measured to assess if the pattern was conserved ($K > 1$), convergent ($K < 1$) or random ($K = 0$). To test for independence in the phylogenetic signals, a generalized least squares (GLS) method was then used to test for relationships between significant traits, subsequently taking phylogenetic relatedness into account with phylogenetic generalized least squares (pGLS) method.

To determine if Diptera communities and functional groups are more or less phylogenetically related than expected by chance several indices were calculated. Faith's phylogenetic diversity metric (PD) (Faith 1992) was calculated for each community. Then a phylogenetic distance matrix from the tree generated was produced with the *cophenetic* function from the package ape (Paradis et al. 2004). The mean pairwise distance (MPD) was calculated as the mean

phylogenetic distance among all pairwise combinations of co-occurring species and the mean nearest neighbor distance (MNTD) was calculated as the mean phylogenetic distance to most closely related species for all co-occurring species (Webb 2000, Webb et al. 2008) with the package *picante*. To analyse the whole community structure, these two metrics were measured among individuals (weighted by abundance) and among species to determine the effect of rare species. For functional groups, only abundance-weighted measures were calculated, because individuals, not species, are filtered and compete in a community (Cornwell and Ackerly 2009, Fine and Kembel 2011). Null models were used to determine if the phylogenetic and functional composition of communities differ significantly from that expected by chance (Gotelli 2000). A null model where taxon labels were randomized 999 times at the tip of the tree, while maintaining species abundance and tree topology was used (Kembel and Hubbell 2006). These 999 null measurements were used to calculate measures of standardized effect size for MPD and MNTD: Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) multiplied by -1 (observed value minus the mean value of the 999 null values divided by the standard deviation of the 999 null values), respectively, and probabilities. Negative NRI/NTI values and high quantiles ($p > 0.95$) indicate phylogenetic evenness, while positive values and low quantiles ($p < 0.05$) indicate phylogenetic clustering, relative to the null model. To determine if the mean NRI and NTI values overall and per wetland class are significantly different among habitats and from zero, t-tests were performed. Trait diversity within communities was calculated in the same way as phylogenetic relatedness, with standardized effect size as a measure of trait dissimilarity among co-occurring species.

2.4.4 Phylobetadiversity

To evaluate the phylogenetic and functional beta dispersion of Diptera communities within and between the three wetland classes, beta phylogenetic differences weighted by abundance were tested using *comdist* (the average MPD for each species in a sample to all species in another sample) and *comdistnt* (the average MNTD for all species in a sample to the nearest neighbors in another sample) using the package *picante*. Bray-Curtis dissimilarity among all sites was calculated as an abundance-weighted measure of betadiversity and pairwise dissimilarities between traits using the function *daisy* with the Gower's distance measure in the package *cluster* (Maechler et al. 2015) were calculated as a measure of trait dispersion among all sites. The

output matrices were used in NMDS ordinations with the *monoMDS* function to determine the differences in phylogenetic community structure using the package *picante*. The function *envfit* was also used to examine the significant relationship between the environmental variables and phylogenetic dispersion, using 999 permutations. To determine if beta and phylobeta diversity were positively spatially autocorrelated, the Mantel statistic in the *ade4* package (Dray and Dufour 2007) was calculated with spatial distance. To assess correlations between species co-occurrence and phylogenetic distances, the Mantel statistic was also performed between a Bray-Curtis dissimilarity matrix and betaphylogenetic and functional dissimilarity matrices.

2.5. RESULTS

2.5.1. Alpha taxonomic structure

A total of 6602 specimens representing 295 species belonging to 28 families were used in analyses (Appendix 2.3). Diptera assemblages varied from 196 to 1645 individuals in each sampling site (Table 2.2). *Scatella stagnalis* Fallén (Ephydriidae) was the most abundant species accounting for 12% of total abundance and was the most widely distributed species, being found in all sites. The next most abundant was *Leptocera erythrocerca* (Becker) (Sphaeroceridae) (8%), followed by *Rachispoda limosa* (Fallén) (Sphaeroceridae), *Incertella bispina* (Malloch) (Chloropidae) and *Elachiptera nigriceps* (Loew) (Chloropidae), together accounting for 4% of the total specimens.

Indicator species analysis revealed that 15 species were significantly associated with one type of wetland and that two were associated with two types. Bog associated species were: *Homoneura sheldoni* (Coquillett) (Lauxaniidae) (IndVal = 0.92, $p = 0.018$), *Euaresta bella* (Loew) (Tephritidae) (IndVal = 0.89, $p = 0.018$) and two Chloropidae: *Malloewia abdominalis* (Becker) (IndVal = 0.9, $p = 0.05$), *Malloewia nigripalpis* (Malloch) (IndVal = 0.9, $p = 0.05$). For marshes the two Ephydrid species *Notiphila avia* Loew (IndVal = 0.89, $p = 0.018$) and *Notiphila olivacea* Cresson (IndVal = 0.87, $p = 0.022$) and a calliphorid species *Lucilia illustris* (Meigen) (IndVal = 0.89, $p = 0.021$) were found to be significantly associated. For swamps, eight species in three families (Sphaeroceridae, Drosophilidae, Ephydriidae) were found as indicators: *Spelobia* sp.A (IndVal = 0.95, $p = 0.02$), *Spelobia luteilabris* (Rondani) (IndVal = 1, $p = 0.009$), *Pterogramma palliceus* (Johnson) (IndVal = 0.96, $p = 0.009$), *Drosophila* sp.2 (IndVal = 0.97, $p = 0.009$),

Drosophila transversa Fallén (IndVal = 0.88, $p = 0.023$), *Chymomyza amoena* (Loew) (IndVal = 0.96, $p = 0.009$), *Athyroglossa granulosa* (Cresson) (IndVal = 0.93, $p = 0.025$), *Ditrichophara exigua* Cresson (IndVal=0.9, $p = 0.045$). Bog and marsh habitats shared *Rhopalopterum carbonarium* (Loew) (Chloropidae) (IndVal = 0.95, $p = 0.035$) while marsh and swamp habitats had *Elachiptera nigriceps* (Loew) (Chloropidae) (IndVal = 0.96, $p = 0.007$) as a mutual indicator species.

2.5.2 Beta taxonomic structure

When testing for the influence of habitat type with ANOVA analyses, relative abundance ($F = 1.63$, $p = 0.25$), observed species richness ($F = 2.14$, $p = 0.173$) and rarefied species richness ($F = 0.69$, $p = 0.52$) (Table 2.2) were not significantly different between wetland types. High turnover of species was observed from week to week in marshes and bogs as supported by NMDS; although in swamps, species compositions from week to week were overlapping (Fig. 2.3A). For the functional groups, the abundance and richness of each trophic group were not significantly different between wetland habitat, and the overall distribution was similar in each habitat. Saprophages were the most abundant and species rich followed by phytophages, predators and parasites (except in bogs where parasites were more diverse than predators). Rare species were less abundant, but more species rich compared to common species and the abundance and richness decreased from small to large sized species (Fig. 2.4).

Community composition shown by NMDS ordination (stress = 0.081) indicated distinct assemblages between the three types of wetlands (Adonis: $R^2 = 0.4$, $p = 0.001$). Species assemblages in each wetland class were associated mainly with local conditions: tree cover ($R^2 = 0.94$, $p = 0.001$), PC1 ($R^2 = 0.9$, $p = 0.001$), conductivity ($R^2 = 0.85$, $p = 0.002$), water above surface ($R^2 = 0.77$, $p = 0.002$), PC2 ($R^2 = 0.74$, $p = 0.004$). Only open water ($R^2 = 0.68$, $p = 0.01$), and exposed land ($R^2 = 0.49$, $p = 0.04$) surrounding the habitats had a lower positive association with marsh and bog respectively (Fig. 2.3B)

2.5.3. Alpha phylogenetic structure

The test of phylogenetic signal using Pagel's lambda showed that the restriction to a wetland type ($\lambda = 0.61$, $\ln L = -238.11$, $\ln L_{\lambda=0} = -240.898$, $p = 0.018$) was significantly non-randomly

distributed over the tree. Blomberg's K value for size ($K = 0.55$, $p = 0.001$) showed that closely related species resemble each other less in size than expected under the Brownian motion model of trait evolution. The GLS of size as a function of wetland type (ANOVA $F = 0.83$, $p = 0.44$) and the pGLS ($F = 0.7$, $p = 0.5$) models were both non-significant.

As expected, Faith's PD showed the same pattern as rarefied species richness as it is highly correlated with species richness, where none of the pairwise comparisons of wetland classes for the entire pool of species or by functional group displayed significant differences ($p > 0.05$). The phylogenetic structure of Diptera communities was never evenly distributed, only a few sites showed clustering and a large proportion showed randomness when compared to phylogenetically random communities generated by the null model. For all sites pooled together, mean NRI value for individuals (2.24, $p = 0.016$) and taxa (2.68, $p = 0.0012$) and mean NTI value for individuals (1.4, $p = 0.01$) and taxa (1.99, $p = 0.0001$) were significantly clustered. At the level of the entire tree, the bog habitat was significantly clustered for co-occurring species ($\text{meanNRI} = 3.9$, $p = 0.026$) but not for co-occurring individuals ($\text{meanNRI} = 2.07$, $p = 0.1$). The other two wetland habitats were not significantly different from a random distribution ($\text{meanNRI} = 0$, $p > 0.05$). Phylogenetic clustering toward the tip of the tree was significant for marsh habitat for individuals ($\text{meanNTI} = 2.29$, $p = 0.04$) and species ($\text{meanNTI} = 2.57$, $p = 0.01$) (Fig. 2.5). The swamp habitat contains species randomly distributed at all level in the phylogeny and for every functional group. The mean NRI for the functional groups showed that bog communities were more closely related than expected for large species (2.5, $p = 0.016$), parasites (2.62, $p = 0.01$) and rare species (2.7, $p = 0.049$) overall and by week (2.06, $p = 0.0009$). The mean NRI value for rare species in marshes by week was also significantly clustered (1.15, $p = 0.0009$). The mean NTI values in marsh habitat showed clustering for medium species (1.76, $p = 0.026$), saprophages (1.72, $p = 0.01$) and rare species (1.97, $p = 0.018$) overall and by week (0.96, $p = 0.00023$) and in bogs for large species (1.46, $p = 0.034$), rare species by week (1.44, $p = 0.00027$) and restricted species (1.99, $p = 0.04$). Standardized effect sizes for all traits pooled were not significantly different from a random expectation.

2.5.4. Beta phylogenetic structure

Mantel correlation between beta and phylobeta diversity were only significantly correlated to

spatial distance for small ($r = 0.32$, $p = 0.032$) and common ($r = 0.31$, $p = 0.01$) species betaNTI values. All Mantel correlations for taxonomic Bray-Curtis vs. phylogenetic diversity and trait dissimilarities were significant. Adonis analyses showed significant differences between types of wetland for all NMDS ordinations except for beta diversity in traits MPD ($R^2 = 0.24$, $p = 0.1$) (Fig 2.6) and beta diversity in common species MNTD/MPD ($p > 0.05$). Overall MPD and MNTD phylogenetic beta diversity were influenced each by a subset of environmental variables influencing taxonomic community structure. MPD beta diversity was affected in decreasing order by conductivity ($R^2 = 0.83$, $p = 0.001$), PC1 ($R^2 = 0.77$, $p = 0.02$), surrounding open water ($R^2 = 0.67$, $p = 0.016$) and tree cover ($R^2 = 0.61$, $p = 0.01$). MNTD beta diversity was influenced in decreasing order by PC1 ($R^2 = 0.9$, $p = 0.001$), tree cover ($R^2 = 0.82$, $p = 0.003$), PC2 ($R^2 = 0.75$, $p = 0.005$), conductivity ($R^2 = 0.68$, $p = 0.011$), surrounding exposed land ($R^2 = 0.62$, $p = 0.025$), surrounding open water ($R^2 = 0.59$, $p = 0.025$) and water above surface ($R^2 = 0.58$, $p = 0.013$). Trait beta diversity was influenced by a subset of environmental variables influencing beta MPD/MNTD (Fig. 2.6).

2.6. DISCUSSION

2.6.1. Taxonomic structure

There was greater similarity within habitat type than among habitats, even the indicator species were found in different families among the three wetland types. Although all indicator species except one (*Euaestha bella*) were saprophagous, and the three wetlands are dominated by saprophages (Fig. 2.4). Predatory species may be underrepresented in this study since species rich wetland predacious families were not sampled such as Dolichopodidae (Pollet 1992), Empididae (Barták and Roháček 1999) and Syrphidae (Castella et al. 1994). Other studies on wetland Diptera showed that communities were dominated by predators followed by saprophages (Beaulieu and Wheeler 2005, Grégoire Taillefer and Wheeler 2012). Saprophagous invertebrate community in wetlands seems to be directly linked to primary production through the detritus food chain (Danell and Sjöberg 1979, Wallace and Webster 1996). In the bog habitat only one species is considered a characteristic inhabitant: *Homoneura sheldoni* (Miller 1977). *Euaestha bella* is a widespread endemic species to North America feeding on the common ragweed *Ambrosia artemisiifolia* L. The two *Malloewia* species are saprophagous in a variety of habitats and widespread in eastern North America. They seem to prefer open habitats such as

wetlands and grasslands (T.A. Wheeler, *pers. comm.*). The two *Notiphila* species associated with marshes are detritus feeders in anaerobic conditions and are obligatory associates with roots of wetland plants (Larson and Foote 1997). *Lucilia illustris* is a widespread species whose larvae are carrion feeders (Florin 2001). In swamps it seems that all indicator species for which ecology is known except one are facultative in wetlands. The only known breeding record of *Athyroglossa granulosa* is from skunk cabbage (*Symplocarpus foetidus*) that grows in wetlands in North America (Grimaldi and Jaenike 1983).

2.6.2. Phylogenetic structure

Environmental filtering acts on the regional scale, as species were phylogenetically segregated in the different wetlands. This is reflected in the phylogenetic signal of the wetland type, the distinct phylobetadiversity and in the different species composition present in each wetland type. At the site scale, phylogenetic clustering tree-wide is argued to result from either radiation or different colonization patterns of habitats in the distant past (Hardy and Senterre 2007, Webb et al. 2008). Ecological-scale community assembly from a species pool that survived the last glaciation is a much more plausible explanation. Most species that survived the last glaciation, the Wisconsin glacial maximum between 22,000 and 14,000 BP, retreated into new niches or found refugia south of the ice sheets (Scudder 1979, Beatty and Provan 2010). By 10,000 BP, the Laurentide ice sheet covering Quebec was reduced by 35% and by 7,000 BP the ice sheet had almost completely receded (Scuderi 2002). The bogs emerged from a very slow peat accumulation process, since the early to middle Holocene (9,000-6,000 BP) in southern Canada (Ovenden 1990, Vitt 1994), which coincided with the Hypsithermal, the warmest time interval of the current interglacial (Pielou 1991). These warmer and drier conditions, permitted dispersal of flora and fauna northward (Hewitt 2000). Consequently, the current distribution of species in bog communities, particularly those with low dispersal range, is still influenced by this past event. During community assembly, environmental filtering first acted on species where plant assemblages (PC1) influenced which traits allowed species establishment. The plant composition is characteristic with only a few species that can survive in these acid and low nutrient conditions. Therefore, the characteristic bog plant species are locally abundant, but do not occur in the surrounding environments. Environmental filtering mostly affected large, parasitic and rare fly species. Several Diptera species are considered peatland specialists (Teskey and Burger 1976,

Miller 1977, Farkas and Brust 1986, Marshall 1994), likely because specialist species survived glaciation in suitable habitats in the southern refugium, and then dispersed northward as the ice receded. In accordance with our hypotheses, we found indications that the bogs support closely related species filtered by harsher environmental conditions, as the entire food web is associated with the water chemistry; peat is acidic in nature and has low available minerals such as nitrogen, calcium, magnesium and phosphorus (Coulsen and Butterfield 1978). This finding is consistent with Silver et al. (2012), who found similar results for Diptera in temporary wetlands. As they start to dry, environmental stresses increase and so increasing phylogenetic clustering is observed. Several authors have suggested that environmental factors at the landscape level may explain more variation in arthropod species composition than local factors (e.g. Økland et al. 1996, Schweiger et al. 2005). Although, in this study the uniqueness of the bog habitat at the landscape level may explain why local variables are more important than surrounding land use for Diptera community composition. Recent turnover of species probably comes from the surrounding exposed lands (e.g. non-vegetated, non-developed, sediments, beaches, burnt area) where Diptera species have environmental requirements suitable for bog habitats. This is in contrast to Savage et al. (2011) who found that species composition in temperate bogs were mostly affected by the presence of a forest buffer in between urban development and agricultural land.

A random structure could result if opposing patterns of clustering and overdispersion are found within the same community (Hardy & Senterre 2007, Mayfield & Levine 2010). Although, at the site scale and at every taxonomic scale, overdispersion was never found. Neutral processes are more important in marshes and swamps, as dispersal limitation may explain species abundance dynamics of small and common species within habitat type as they are affected by the inter-site distances (Condit et al. 2002). The assembly of marsh communities may be seen as recent processes with a balance between neutral processes and environmental filtering, where species emigrate from surrounding lentic habitats and are filtered by the variation in the water level. Species must be adapted to survive the variation in the hydrological cycle or disperse to more suitable habitats (Murkin and Batt 1987). The assembly of swamp habitats can be seen as solely neutral processes as this habitat is more heterogeneous and shares more characteristics with the surrounding environment such as forests, for the tree cover, and water bodies, for the higher mineral content (National Wetlands Working Group 1997).

However, the detailed life-history and ecological traits that confer habitat preference for Diptera species in bogs and marshes were not measured, as the functional status of a large number of species is unknown because of insufficient ecological knowledge. Nonetheless, it is probably reasonable to assume that closely related species share important unmeasured traits showing potentially strong phylogenetic signals, so the degree of phylogenetic relatedness can possibly be used as a proxy for ecological similarity as all significant traits showed clustering in NRI and NTI values. Poff et al. (1997) analyzed quantitatively evolutionary lability of traits and found that life-history (e.g. voltinism, synchronization of emergence) were more evolutionary constrained than ecological traits (e.g. trophic habit, thermal preference), probably because life-history traits are associated with the reproductive success, thus the persistence of species. Behavioural (e.g. specialization) and feeding related traits have been found to be involved in habitat selection at smaller scales; while size, dispersal ability and the number of generations per year have been associated with larger scales (Larsen and Ormerod 2010). No phylogenetic signal for diet overall was found, although one could potentially be found at a lower level as these broad categories can be divided in several subcategories (e.g. saprophages can be divided into detritus feeders, coprophages, bacterial feeders, secondary invaders of damaged plants, etc.). Even if a phylogenetic signal is not detected in a community as a whole, it might exist within a clade (Losos 2008).

2.6.3. Taxonomic vs phylogenetic structure

The three types of wetlands studied are distinct in terms of their taxonomic and phylogenetic community structure and trait composition within particular terminal clades (although the clades are spread out on the entire phylogeny, resulting in similar trait MPD phylobetadiversity across wetland types). However, the relative abundance, species diversity and functional trait distribution are similar among habitats. Trends of the changes in beta diversity with the wetland gradient are similar when either measured taxonomically or phylogenetically. Without examining phylogenetic relatedness, we would have concluded that high species turnover and random functional turnover indicate stochasticity in species turnover and community assembly, owing to dispersal limitation (Swenson et al. 2010). Phylogenetic analyses in complement with ecological metrics have been shown to report an effect of treatments when classical metrics (abundance,

diversity) do not (Kelly et al. 2015). No change in alpha diversity, abundance or functional diversity along this environmental gradient could be explained by functionally similar species replacing each other in the communities and that flies perceived their environment at a smaller scale than humans.

2.6.4. Rarity effect

Rarity is an important concept in community ecology and no consensus has been reached about the mechanisms underlying abundance of species. According to several authors, rare species are assembled by niche differentiation and specialization, and/or temporal resource partitioning which differ from environmental preferences or dispersal limitation of common species (e.g. Kunin 1997, Chesson 2000, Magurran and Henderson 2003). The niche differentiation hypothesis suggests that three predictions must be followed. First, a phylogenetic signal of abundance is expected. Second, rare species should contribute more to community phylogenetic diversity and third, phylogenetic dissimilarity should be observed within and between assemblages of common and rare species (Mi et al. 2012). Our findings support this hypothesis. On average, species present in one wetland type tended to be distantly related to species present in two or three types as a phylogenetic signal was found. Rare species assemblages had higher cumulative phylogenetic diversity for nine of twelve sites than common species assemblages which were all randomly distributed. Rare species assemblages showed clustering in marsh and bog habitats and by week, while common species distribution was always random and influenced by dispersal limitation. In accordance with Thompson and Townsend (2006), this shows that local ecological factors and dispersal limitation play equally important roles in macroinvertebrate distribution. The rarity effect revealed hidden patterns, that different processes affect the occurrence of species and the local dominance as suggested by Chalmandrier et al. (2015). The different patterns of spatial partitioning along this wetland gradient suggest that niche differentiation by temporal partitioning of the active season may contribute to the high diversity of rare species in these communities.

Size is usually used as a proxy for dispersal capacity, here we can consider the use of a morphological surrogate for ecology as small species are affected by spatial distances. Low phylogenetic signal in a trait is usually considered as evolutionary lability (Blomberg et al. 2003,

Silvertown et al. 2006), although the evolutionary process underlying this lability is difficult to detect (Revell et al. 2008). Errors in phylogenetic topology as well as estimation of species means will downwardly bias the calculation of phylogenetic signal (Blomberg et al. 2003, Ives et al. 2007). In this study the hypothesized phylogeny was constructed with one gene; although most of the species were clustering by family. The average size for species was measured from a mean of two mounted individuals which could have brought some variation and lowered the phylogenetic signal. Although even when size was treated as a categorical trait with ranges to incorporate this variation, no phylogenetic signal was found.

2.7. CONCLUSIONS AND CONSERVATION IMPLICATIONS

Phylogenetic community structure analyses revealed high value and complementarity with standard measures of community assembly in explaining patterns of species variation within and across wetland habitat types. Results showed that Diptera communities exhibit phylogenetic structure in wetlands and phylogenetic clustering meaning that environmental filtering increases with environmental extremes. We found evidence that rare Diptera species have unique habitat requirements and that the high diversity is maintained by temporal turnover of species with similar traits filtered by the environment. The species composition differed highly among the three wetland types, suggesting that maintaining a diversity of wetland habitats within a region is of major importance for species diversity. Also, results suggest that human interventions aimed at conserving and restoring wetland structure and function need to vary the focus of attention in the different wetland types. When neutral assembly processes are important, restoration projects will have to consider stochasticity and may require intervention (such as propagule addition or removal) (Grégoire Taillefer and Wheeler 2013). On the other hand, when niche processes are more important, restoration projects will have to focus on desired habitat properties for species of interest. The wide range of wetland site size (6.7 to 161.6 ha) did not influence the diversity and abundance of Diptera, which was similar to results found by Savage et al. (2011). Area has been found to influence predacious long-legged fly (Decler et al. 2015), so the effect may vary with size and specialisation and be obscured in these functionally diverse communities. Local characteristics are the major determinants of composition. We could argue that even small fragments of wetlands are of major importance to maintain high diversity and abundance of Diptera. This is in line with Perović et al. (2015) who showed that maintaining a higher level of

landscape complexity with many small important habitat patches for butterflies was maintaining increased taxonomic and functional diversity. More configurational heterogeneous landscapes are shown to support more microhabitats thus more species with different ecological functions (Devictor and Jiguet 2007, Fahrig et al. 2011). As Diptera are a link between primary producers and higher food web levels, they can have an impact on ecosystem services because they serve, for example, as food resources to wetland inhabitants such as waterfowl, fish, amphibians, birds, mammals and other insects. Finally, this study emphasizes on local scales, but what about assemblages of species in wetlands within a large geographical area? A broader analysis applying the same approaches as above could make the link between phylogenetic community structure and macroecology as well as addressing how assemblages vary across space.

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Table 2.1. Ground cover variables reduced with principal component analysis. Variables with loadings larger than 0.32 in principal components (PC) 1 to 4 are in bold.

Variables	PC1	PC2	PC3	PC4
<i>Abies balsamea</i>	-0.31	0.43	0.00	0.47
bare soil	-0.31	0.08	-0.01	-0.53
<i>Betula alleghaniensis</i>	-0.31	0.43	0.00	0.47
<i>Betula populifolia</i>	0.23	0.00	-0.01	-0.02
? <i>Calla palustris</i>	-0.31	0.43	0.00	0.47
<i>Carex oligosperma</i>	0.46	0.16	-0.40	0.02
<i>Carex viridula</i>	-0.31	0.43	0.00	0.47
<i>Cephalanthus occidentalis</i>	-0.23	-0.12	-0.01	-0.18
<i>Chamaedaphne calyculata</i>	0.52	0.17	-0.28	0.03
<i>Cornus stolonifera</i>	-0.17	-0.09	-0.02	0.11
dead wood	-0.37	-0.06	-0.02	0.02
<i>Drosera rotundifolia</i>	0.28	0.07	-0.05	0.03
<i>Equisetum pratense</i>	-0.46	0.49	0.00	0.03
<i>Eriophorum vaginatum</i>	0.49	0.09	0.46	0.06
<i>Fraxinus nigra</i>	-0.23	0.29	0.02	-0.55
<i>Hydrocharis morsus-ranae</i>	-0.28	-0.61	-0.12	0.07
<i>Kalmia angustifolia</i>	0.37	0.05	0.55	0.05
<i>Larix laricina</i>	0.14	-0.03	0.09	-0.01
<i>Ledum groenlandicum</i>	0.29	0.05	0.40	0.05
litter	-0.47	-0.03	0.11	-0.08
<i>Lysimachia terrestris</i>	0.34	0.15	-0.54	-0.01
<i>Onoclea sensibilis</i>	-0.49	0.35	0.01	-0.28

Open pool	-0.51	-0.33	-0.11	0.33
<i>Osmunda regalis</i>	-0.28	0.25	0.02	-0.57
<i>Phalaris arundinacea</i>	-0.10	-0.40	-0.08	0.12
<i>Phragmites australis</i>	-0.17	-0.09	-0.02	0.11
<i>Pinus rigida</i>	0.34	0.15	-0.54	-0.01
<i>Pleurocarpus moss</i>	-0.65	0.15	-0.05	0.04
<i>Polytrichum</i> spp.	0.58	0.13	0.34	0.05
<i>Sagittaria latifolia</i>	-0.18	-0.40	-0.08	0.02
<i>Salix pedicellaris</i>	0.20	0.01	0.33	0.01
<i>Salix pyrifolia</i>	0.34	0.15	-0.54	-0.01
<i>Sphagnum</i> spp.	0.66	0.19	-0.05	0.04
<i>Spiraea alba</i>	0.34	0.15	-0.54	-0.01
<i>Spirodela polyrhiza</i>	-0.14	-0.50	-0.10	0.10
<i>Toxicodendron radicans</i>	-0.37	0.49	0.02	-0.23
<i>Typha angustifolia</i>	-0.14	-0.52	-0.10	0.11
<i>Vaccinium ?angustifolium</i>	0.29	0.05	0.40	0.05
<i>Vaccinium myrtilloides</i>	0.20	0.01	0.33	0.01

Table 2.2. Abundance (N), species richness (S_{obs}) and rarefied species richness \pm standard error (S_{est}) for each of the 12 wetland sites. Rarefied species richness was standardized at 196 individuals (PIN_BG).

Site	N	S_{obs}	S_{est}
CAL_SW	532	73	49.2 \pm 3.1
TIH_SW	1646	105	38.4 \pm 3.7
OKA_SW	903	86	43.6 \pm 3.5
LAZ_SW	234	62	57.6 \pm 1.8
BER_MA	258	52	46.5 \pm 2
OKA_MA	545	56	33.6 \pm 2.9
MIL_MA	1037	91	46.2 \pm 3.5
FOR_MA	252	33	30.5 \pm 1.4
BLA_BG	237	30	27.5 \pm 1.4
PIN_BG	196	40	40 \pm 0
MIR_BG	290	67	56.2 \pm 2.6
BRB_BG	468	72	45.5 \pm 3.3

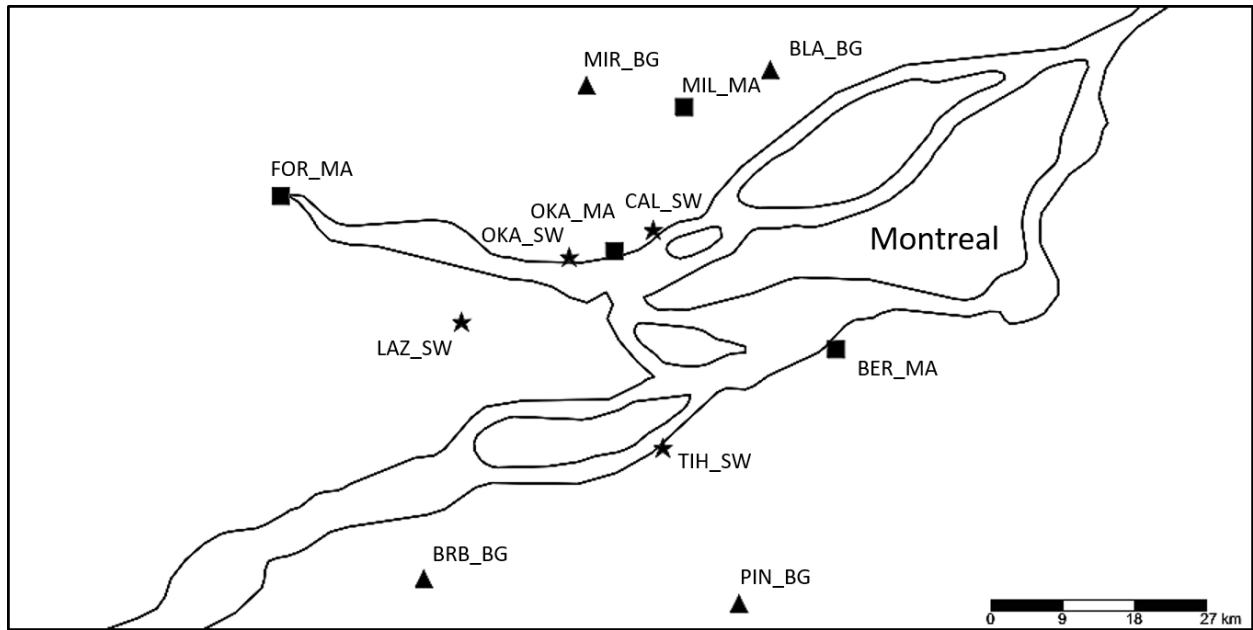


Figure 2.1. Map of the 12 study locations in the Montreal metropolitan area and surroundings, Quebec, Canada. Stars: swamps; squares: marshes; triangles: bogs. (CAL_SW: Pointe-Calumet swamp; TIH_SW: St-Thimothé swamp; OKA_SW: Oka National Park swamp; LAZ_SW: St-Lazare swamp; BER_MA: Ile St-Bernard marsh; OKA_MA: Oka National Park marsh; MIL_MA: Mirabel Parc du Domaine Vert marsh; FOR_MA: Pointe-Fortune marsh; BLA_BG: Blainville bog; PIN_BG: Pin-Rigide bog; BRB_BG: Ste-Barbe Large Tea Field bog; MIR_BG: Mirabel bog). Map created with SimpleMappr (www.simplemappr.net).

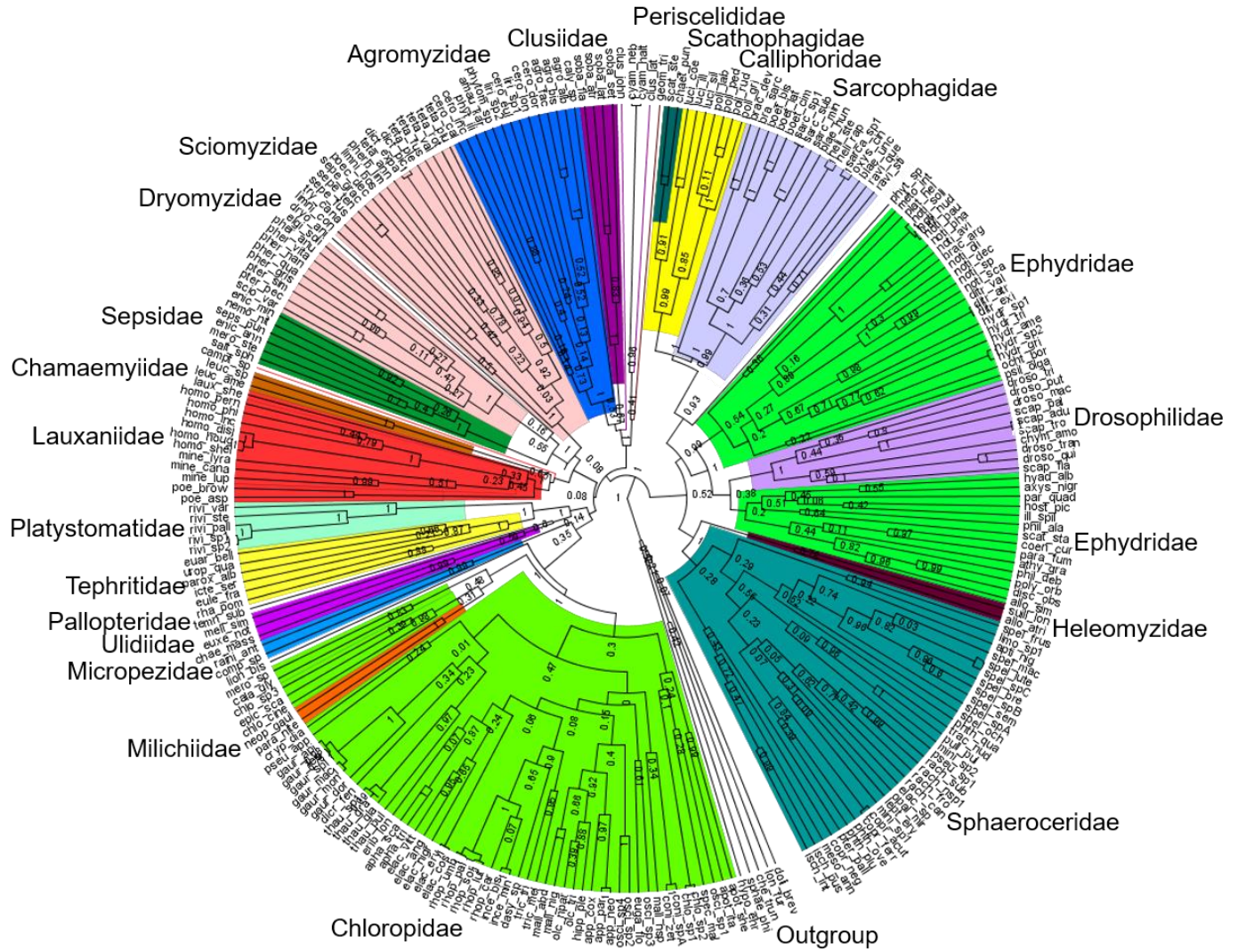


Figure 2.2. Hypothesized phylogenetic relationships, based on CO1, among Schizophora (Diptera) species collected in the 12 wetlands. Colours represent families, branch lengths represent divergence time estimates and numbers on nodes represent posterior probabilities. Species codes are in Appendix 2.3

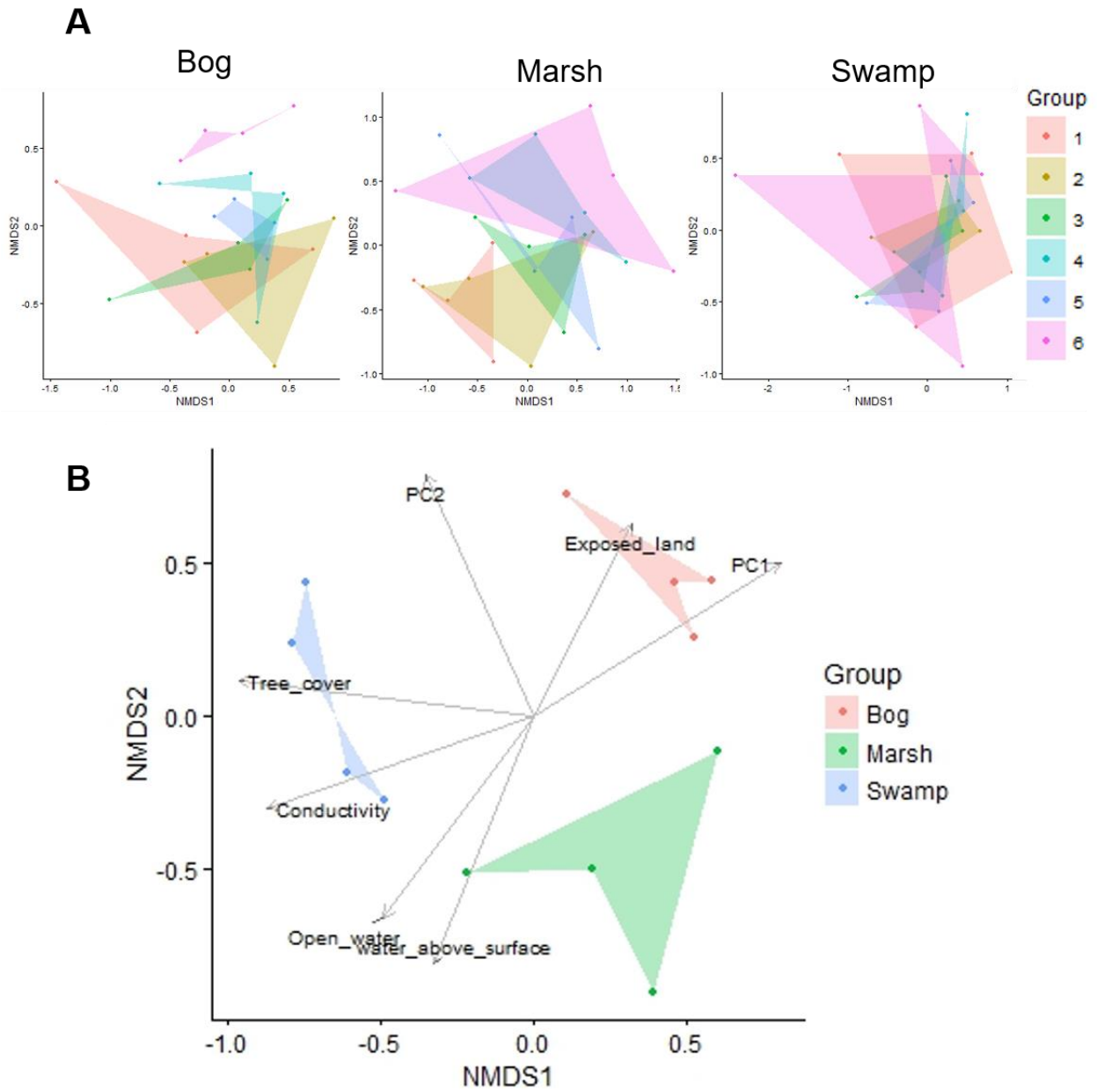


Figure 2.3. Non metric multidimensional scaling ordination of Diptera species collected A) by week in each wetland type and B) overall in the three types of wetlands. Arrows represent vectors of the seven variables that explain Diptera species composition.

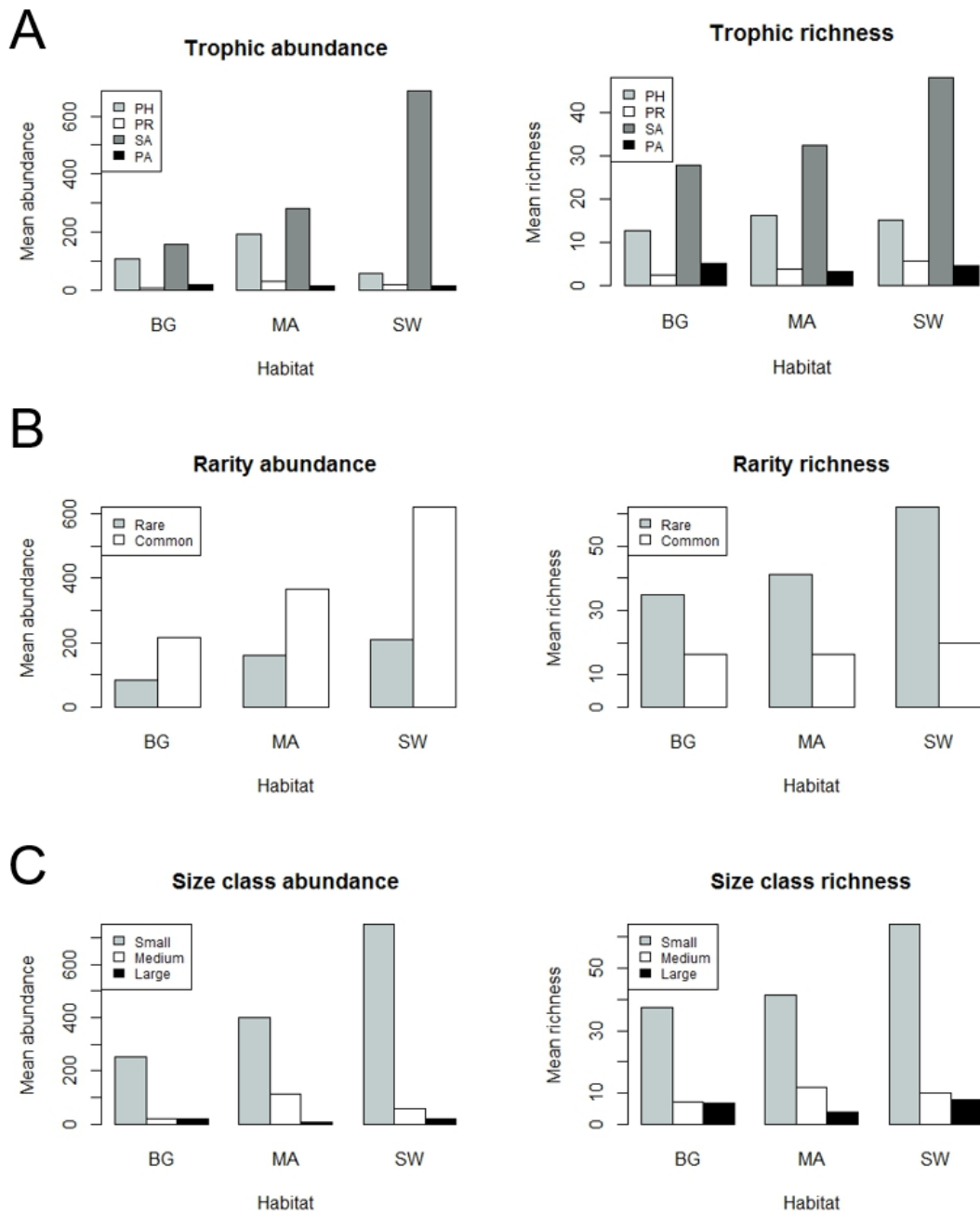


Figure 2.4. Changes in A) Trophic mean abundance and richness; B) Rarity mean abundance and richness; and C) Size class mean abundances and richness of Diptera between bogs (BG), marshes (MA) and swamps (SW).

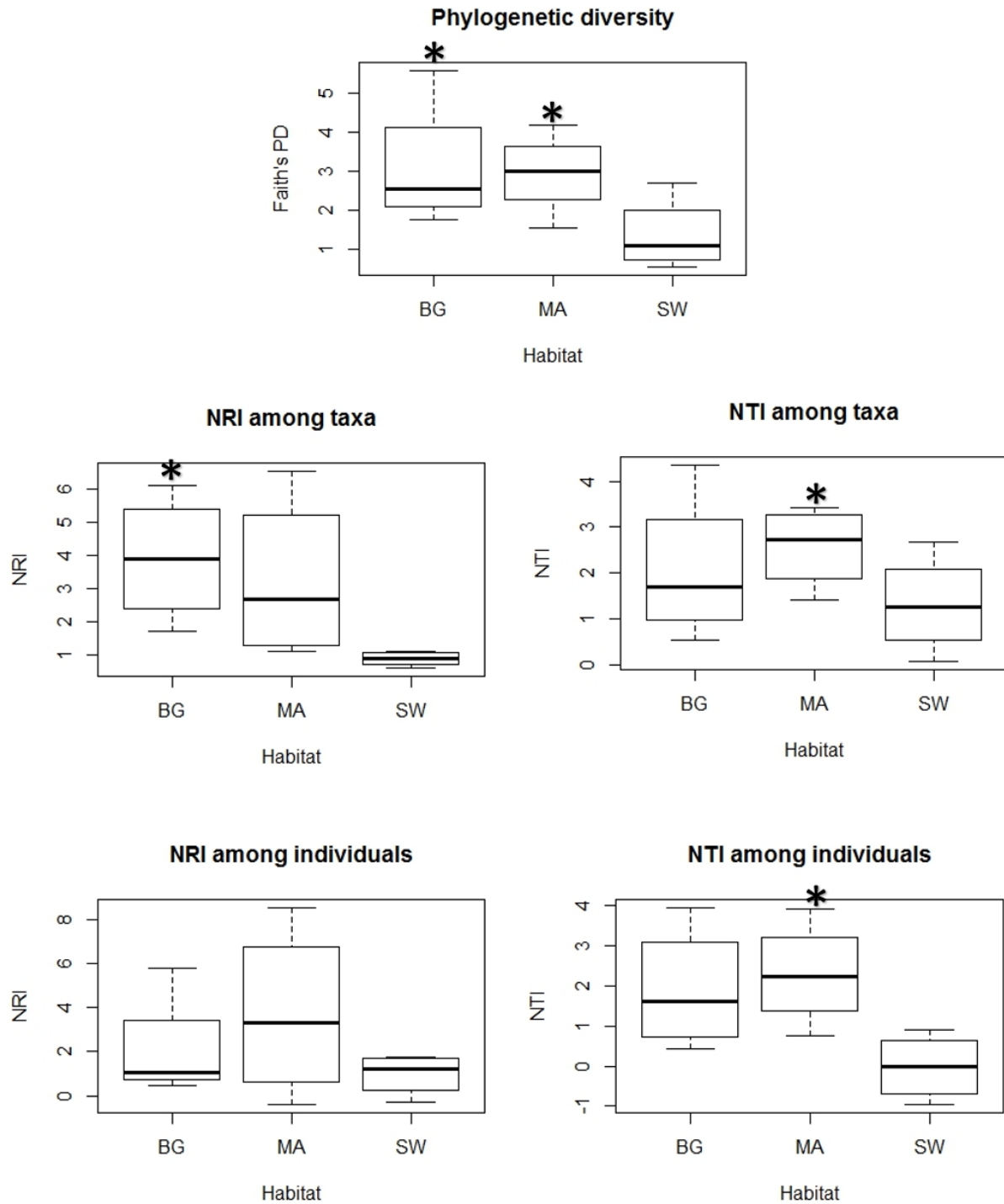


Figure 2.5. Distribution of mean \pm standard deviation of phylogenetic diversity, net relatedness index (NRI) and nearest taxon index (NTI) of Diptera across the three wetland types (BG: bog, MA: marsh, SW: swamp). * Significant deviation from 0 (t-test) at $p < 0.05$.

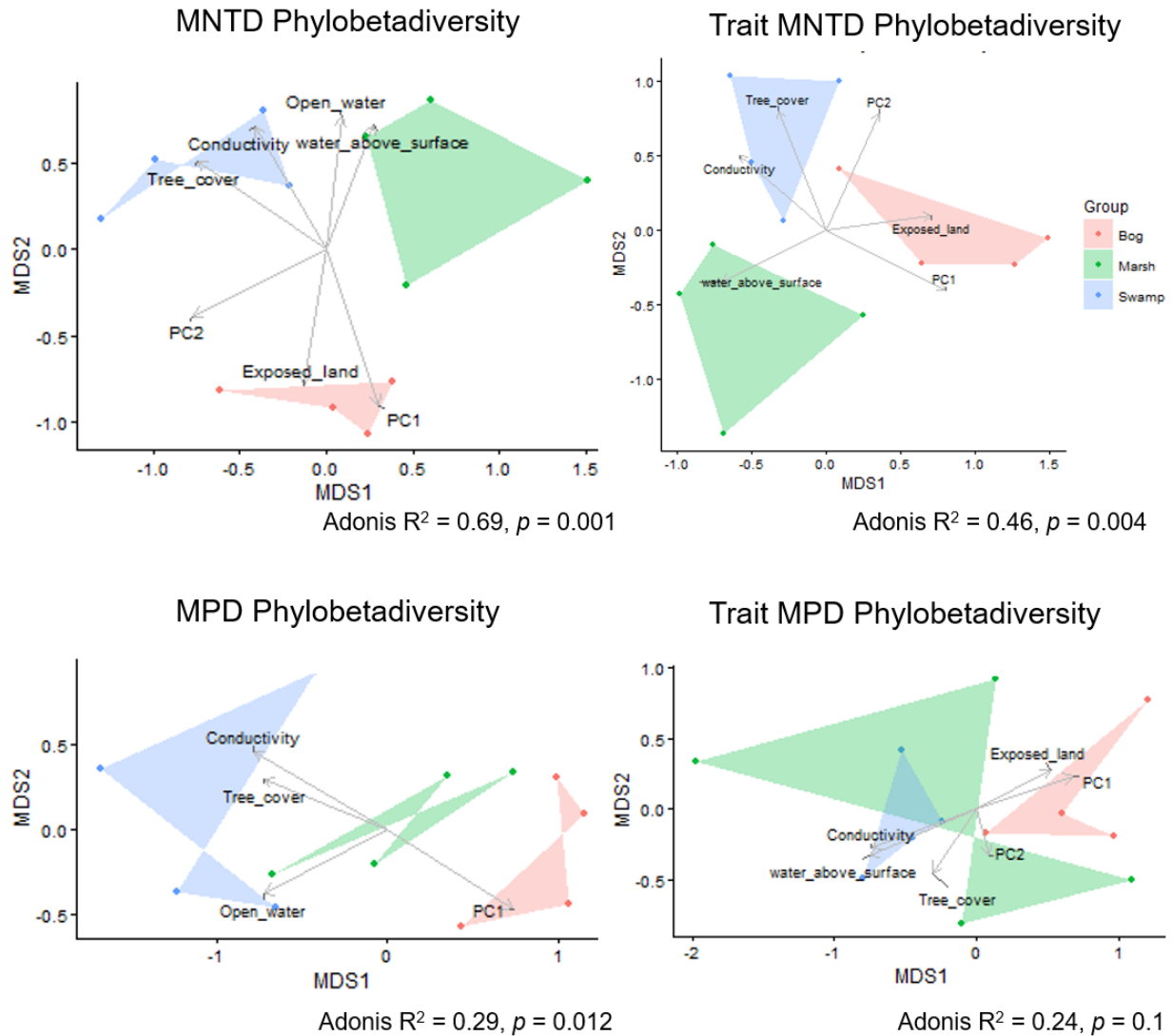


Figure 2.6. Non metric multidimensional scaling ordination of species and trait phylogenetic beta diversity of mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) of Diptera in the three types of wetlands. Arrows represent vectors of the variables that explain phylogenetic turnover in community composition.

2.10. CONNECTING STATEMENT

In Chapter 2, I examined the taxonomic, phylogenetic and functional structure of twelve Diptera communities in three types of wetlands. I assessed rarity patterns, beta- and phylobeta- diversity and tested their relationships with environmental variables. I found that rare species tended to be distantly related to common species as a phylogenetic signal was found. Bog habitats supported closely related species filtered by harsher environmental conditions, while neutral processes were increasingly important from marshes to swamps, as dispersal limitation explained species abundance dynamics. Clustering, thus environmental filtering, increased with environmental extremes.

This chapter emphasized patterns at local scales, but what about assemblages of species in wetlands in a large geographical area? In Chapter 3, a broader analysis using a similar sampling method as Chapter 2 was applied to a single wetland type: bogs, across three different ecoregions in Quebec and across three spatial scales. In replacement of non-metric multidimensional scaling, redundancy analysis for species composition and distance-based redundancy analysis for functional and phylogenetic compositions were used with variation partitioning to test the relative influence of environmental, spatial and climatic variables on community structure. This will help to make the link between phylogenetic community structure and macroecology as well as addressing how assemblages vary across space and what influences their distribution.

CHAPTER 3: Latitudinal patterns in phylogenetic and functional diversity of Diptera in temperate bogs

3.1. ABSTRACT

Conservation of biodiversity is growing in interest, and wetlands are disappearing at an alarming rate, so understanding how communities are assembled and how interactions among species and ecosystems influence evolution is critical to management of threatened habitats. Here, we compared species and functional diversity and assemblages of peatland Diptera within and between ecoregions in Quebec, Canada. We then determined if the phylogenetic structure of peatland Diptera communities was clustered, overdispersed or random and whether the structure differed with spatial scale (trap, site, ecoregion). Finally, we tested alpha and beta diversity along environmental and spatial gradients to determine which processes influence Diptera communities and diversity. We found that the major forces structuring Diptera assemblages in bogs across Quebec are stochastic processes, such as dispersal limitation. However, those random patterns change to environmental filtering with anthropogenic disturbances modifying the landscape. Bogs across the three ecoregions support similar abundance, species richness and functional diversity. Assembly rules are mostly dictated by patch and landscape parameters specific to each ecoregion affecting dispersal and establishment between sites. This suggests that the three levels of diversity studied are complementary and give a different picture of macroecological patterns in these threatened habitats. It also shows that conservation of mobile organisms in habitats such as bogs will depend on conservation plans focusing on both patch quality and surrounding landscape, and that different conservation strategies need to be applied in different ecoregions.

Key words: community phylogenetics, environmental filtering, stochasticity, biodiversity, anthropogenic disturbances, spatial structure, trait-based community assembly

3.2. INTRODUCTION

Taxonomic, functional, and phylogenetic diversity are complementary metrics that can be used to quantify different components of biodiversity (Petchey & Gaston 2002, Magurran 2004, Cadotte et al. 2010). Taxonomic diversity indices treat species as ecologically equivalent and evolutionary independent (Swenson et al. 2012). Variation in species composition and traits

across species are influenced by their ecology and evolutionary history (Freckleton & Jetz 2009). Functional diversity indices use life-history or biological traits of species that can influence their occurrence within a particular environment (Tilman 2001). Phylogenetic diversity indices measure evolutionary factors that affect the ecological relationship between species (Webb 2000).

Two evolving and complementary fields have made progress in explaining how local communities are assembled from the regional species pool: metacommunity ecology and community phylogenetics. Metacommunity ecology aims to predict species distribution, abundance and interactions on a variety of spatial and temporal scales (Leibold et al. 2004, Gravel et al. 2006). Alternatively, community phylogenetics measures how species traits and relatedness explain patterns of community structure in an evolutionary framework (Webb 2000, Cavender-Bares et al. 2009, Peres-Neto, Leibold & Dray 2012). Two theoretical approaches have primarily been used to explain the distribution of species in communities: niche (Diamond 1975, Webb 2000) and neutral (Bell 2001, Hubbell 2001) models. The evolution of species traits, environmental filtering and competitive exclusion are processes that can structure a community in a phylogenetic context, with constituent species phylogenetically clustered or overdispersed, supporting the niche model. In contrast, a random pattern of phylogenetic relationships in a community can indicate that these processes are not dominant in structuring the community and that species are instead dispersing at random from the metacommunity, thus supporting the neutral model (Hardy & Senterre 2007). The neutral model makes the assumption that all species in a community are ecologically equivalent and that stochastic processes - birth, death, dispersal and speciation - dominate over deterministic forces, such as competition or other species interactions (Hubbell 2001). The distribution and abundance of organisms are influenced by different forces at different spatial and temporal scales. At regional scales, biodiversity patterns can be shaped by evolutionary and ecological factors such as environmental heterogeneity, speciation and trait evolution. At local scales, biotic interactions, microhabitat heterogeneity and functional traits may be more important factors influencing community composition (Graham & Fine 2008, Kraft & Ackerly 2010).

Because environmental properties are set in a landscape context and anthropogenically-mediated changes are also known to influence species and functional richness and turnover, different

scales may filter species traits to influence trait composition in local communities (Poff 1997). An organism possesses a combination of traits, some of which can be concordant with phylogeny while others are independent. This allows the application of a trait-based approach across biogeographic boundaries in similar habitats having a different species pool (Lamouroux, Poff & Angermeier 2002, Grégoire Taillefer & Wheeler 2012).

In this study, we use a multimetric approach to assess composition and diversity of insect communities in peatlands across multiple ecoregions in Quebec, Canada. Quebec covers 1.7 million km², and a strong latitudinal gradient of both climatic conditions and human occupancy influence the distribution of vegetation and animals. Peatlands cover 7- 9% of the province (Buteau 1988) and, although they have important ecosystem functions in improving water quality, protecting shorelines, stabilizing water supplies, moderating the effects of floods, and recharging groundwater aquifers ((Keiper, Walton & Foote 2002), they are a threatened ecosystem in Quebec. Due to the limited amount of research on insects in these habitats, our understanding of their ecological roles and species composition is incomplete. The lack of taxonomic resolution, available identification tools or ecological knowledge partly explains why terrestrial arthropods are not as widely used in conservation studies as other taxa (e.g. New 2007) even if arthropod species represent 65% of the world's documented biological diversity (Groombridge & Jenkins 2002).

Flies (Diptera) are an ideal taxon for studying taxonomic and phylogenetic community composition in peatlands at broad spatial scales. Diptera are abundant, species-rich, and ecologically and trophically diverse in peatlands (Blades & Marshall 1994, Pollet 2001, Keiper, Walton & Foote 2002, Grégoire Taillefer & Wheeler 2012). Diptera are associated with a variety of terrestrial, semi-aquatic or aquatic peatland habitats including: mud shores, vascular plants, decaying organic matter, emergent vegetation, macrophytes, and algal mats (Ferrar 1987, Keiper, Walton & Foote 2002). Some Diptera species are peatland specialists, either because their larval or adult food resource or breeding media are restricted to or characteristic of peatlands (Teskey 1969, Teskey & Burger 1976, Farkas & Brust 1986, Marshall 1994). At local spatial scales, vegetation composition and substrate quality have been found to influence Diptera composition and trophic groups (Figueiro et al. 2012, Grégoire Taillefer & Wheeler 2012). At regional scales,

Alves de Mata et al. (2010) suggested that Diptera are correlated with vegetation composition, while Patitucci et al. (2011) found that assemblages were best explained by urbanization, latitude, temperature and elevation. Økland et al. (2005) suggested that climate, spatial (longitude) and landscape variables were important for Diptera assemblages.

Only a few studies have examined the diversity of wetland Diptera (e.g., Blades and Marshall 1994, Barták & Roháček 1999, Beaulieu & Wheeler, 2001, Grégoire Taillefer & Wheeler 2010-2012-2013, Savage et al. 2011) and even fewer have looked at their phylogenetic community structure (Pfenninger et al. 2007, Espíndola et al. 2012, Silver, Vamosi & Bayley 2012). Our model group was a few selected families within Schizophora that encompasses a large range of life-history and biological traits, and which are abundant and species rich in peatlands.

Consequently, we proposed to study the taxonomic, functional and phylogenetic composition and diversity patterns of peatland Diptera in three Quebec ecoregions, arranged broadly from south to north. We compared species and functional diversity and assemblages of peatland Diptera within and between ecoregions. We then determined if the phylogenetic structure of peatland Diptera communities was clustered, overdispersed or random and whether the structure differed with spatial scale (trap, site, ecoregion). Finally, we tested taxonomic, functional and phylogenetic alpha and beta diversity along environmental and spatial gradients to determine which processes influence Diptera communities and diversity.

We tested three hypotheses on Schizophora (Diptera) diversity patterns between the three ecoregions: 1) Species richness will increase from north to south and differences in trait and species composition will be mostly related to climate. Smaller and more disturbed wetlands will be characterized by lower overall trait diversity and dominated by species possessing traits related to higher resilience: smaller body size, shorter life cycles and good dispersal ability. 2) Coexisting species at the local scale will exhibit more phylogenetic overdispersion or random dispersion, and clustering will increase with increasing spatial scale. More anthropogenically transformed landscape matrices will support increasing phylogenetic clustering. 3) Species and phylogenetic beta diversity at the landscape scale will be related to local characteristics such as soil cover composition and surrounding characteristics such as community isolation, wetland size and/or percentage of surrounding forest and wetlands. At the regional scale, climate will explain

the most variation in species and phylogenetic beta diversity.

3.3. MATERIALS AND METHODS

3.3.1. Study sites, sampling and processing

Study sites were five peatlands in each of three ecoregions (Ricketts & Himhoff 2003) (Fig. 3.1): Eastern Canadian Forest (Montreal Metropolitan area and surroundings, 45.2° N, 73.9° W) (Region code: Montreal, MTL); Eastern Great Lakes Lowland Forest (Saguenay area, 48.8° N, 72.2° W) (Region code: Saguenay, SAG) and Central Canadian Shield, southern James Bay area, 49.8° N, 77.2° W) (Region code: James Bay, BJM). To standardize the peatland type across the ecoregions, we selected open raised bogs with pH < 4.5 dominated by *Sphagnum* mosses, ericaceous shrubs, a tree cover of less than 30% and no open pools of water. Sites in the Eastern Canadian Forest ecoregion were chosen from high resolution digital aerial photos available from Ducks Unlimited Canada (Beaulieu et al. 2010) and through communication with experts. Sites in the Eastern Great Lakes Lowland Forest ecoregion were chosen from peatlands inventoried by Calmé, Desrochers & Savard (2002). Sites in the Central Canadian Shield ecoregion were chosen in the field by driving along the James Bay Road (Route de la Baie-James).

Sampling was conducted weekly for five weeks during the period of highest Diptera species richness and activity. Montreal sites were sampled from 28 June to 31 July 2013, Saguenay sites from 2 July to 8 August 2014, and James Bay sites from 29 June to 29 July 2015. In each site, samples were collected using yellow pan traps and sweeping in an area of 30 m x 30 m, at least 30 m from the edge. Sweep samples were collected weekly on three random transects of 20 m with 20 sweeps on each transect in suitable weather conditions. Three transects of four pan traps each were placed 10 m apart in the 30 m x 30 m plot. Pan traps were yellow plastic bowls placed in the soil with their upper rim flush with the ground surface and filled with a 50% solution of propylene glycol and water, with a drop of liquid detergent as a wetting agent. Pan traps were serviced every 6-8 days.

Insects were preserved in 95% ethanol for subsequent DNA extraction. Small flies were dried using hexamethyldisilazane, and then mounted; larger flies were transferred into ethyl acetate, then pinned and air-dried. Specimens were deposited in the Lyman Entomological Museum

(McGill University, Ste-Anne-de-Bellevue, QC). Target taxa were identified to named species or morphospecies. Each species was assigned to a category in each of eight biological traits: feeding habits, size, specialization, habitat preference for oviposition, preferred substrate, voltinism, overwintering stage, temperature range, wetland specialization. Also, three indirect rarity measures were used: frequency of occurrence, range, rarity (Table 3.1). Trait values were determined from direct measurements/counts, published literature and consultation with Diptera specialists.

3.3.2. Habitat and vegetation variables

At the local scale, the following ground cover attributes were surveyed at week three in five 1 m x 1 m quadrats placed at each corner and in the middle of the 30 m x 30 m area at each site: percent plant species cover, litter cover, canopy cover, open water cover and bare soil cover. Fluctuation of water-table depth (cm) was estimated with the PVC tape discoloration method (Belyea 1999). PVC tape was mounted along 1 m long bamboo sticks, one of which was inserted vertically in each site with 15 cm left above the surface and left for the five weeks of sampling. Chemical parameters of the substrate (pH, conductivity and temperature) were measured with Hanna pocket EC/TDS and pH Tester in the field at week three at two locations within the 30 m x 30 m area.

At the regional scale, wetland size and the nature of the surrounding matrix were quantified using QuantumGIS version 1.8.0 (Quantum GIS Development Team 2012) software with the Earth Observation for Sustainable Development of Forests (EOSD) land cover datasets of circa year 2000 representing 23 land cover classes at a spatial resolution of 25 m (Wulder et al. 2008). Land use (open water, exposed land, urban development, low vegetation, wetland, forest, agriculture) surrounding each wetland was measured in m² within a circle with a 2 km radius. Diptera have been found to respond to the surrounding matrix at this scale (Meats & Smallridge 2007, Savage et al. 2011). Climatic variables that are known to influence arthropod diversity (Bowden & Buddle 2010) were also extracted from WorldClim version 1.4 (Hijmans et al. 2005) in 30-arcsecond resolution. Values at the site locations were extracted with raster, rgdal and foreach packages in R version 3.2.2 (R Development Core Team 2015). The seven variables selected were: annual mean temperature, maximum and minimum temperature of the warmest

and coldest month, mean temperature of coldest and warmest quarter, temperature seasonality (standard deviation *100) and annual precipitation.

3.4. STATISTICAL ANALYSES

3.4.1. Taxonomic and functional composition

Communities in each peatland (Appendix 3.1) were characterised by relative abundance (Abun), observed species richness (S), diversity (S_{rare}) and extrapolated species richness (Chao1) from samples pooled by sites throughout the season. Diversity was assessed with rarefaction curves based on 1000 permutations with species richness as a diversity index. Extrapolated species richness was assessed using a bias-corrected Chao index (O'Hara 2005). Significance of differences in relative abundance and species richness indices among ecoregion was determined based on ANOVA *F* tests. All analyses were performed using the R vegan package (Oksanen et al. 2012).

Functional diversity, which considers the distribution and range of functions of co-occurring species (Appendix 3.2) in a community, was measured with three multidimensional indices (Villéger, Mason & Mouillot 2008). Functional Richness (FRic) was standardized by the total FRic to constrain the values between 0 and 1, Functional Evenness (FEve) and Functional Divergence (FDiv) were weighted by the abundance of species. First, a Gower dissimilarity matrix was computed via gowdis (Podani 1999) because traits were quantitative and categorical, and lingoes corrections were applied to obtain Euclidean distance matrices. Dimensionality of the trait matrix was reduced to 40 out of 157 PCoA axes due to computational power limitations. Significance of differences between sites and ecoregion were determined with ANOVA *F* tests. Community-level weighted trait means (CWM) (Lavorel et al. 2008) were used to determine dominant functional composition at each site, where quantitative traits are weighted by abundance and categorical traits are returned as the dominant category. All analyses above were computed with the function *dbFD* of the FD package (Laliberté et al. 2014).

Redundancy analysis (RDA) was used to test for the similarity in overall taxonomic and functional structure and for the relationships between species and functional assemblages to environmental variables (Appendix 3.3) using the vegan package. Prior to RDA, species

abundances were Hellinger transformed (Legendre & Gallagher 2001). A principal coordinate analysis (PCoA) of the dissimilarity matrix (via *gowdis*) of CWM was computed, principal coordinates eigenvalues of CWM were use as response variables in the subsequent RDA. Principal component analysis (PCA) was used to reduce the number of ground cover variables. Significant axes were identified with the Kaiser-Guttman criterion (Yeomans & Golder 1982), and the first five significant PCA axes retained 82% of variation explained (Appendix 3.4). To reduce the number of environmental variables in the subsequent analyses and to avoid autocorrelation between them, remaining environmental variables were observed with scatterplots. Only annual temperature and soil temperature were removed. Latitudes and longitudes were transformed into corresponding coordinates in X (east-west) and Y (north-south) distances using the function *geoXY* in the package *SoDA* (Chambers 2008). Forward selection of explanatory variables was applied with the function *forward.sel* of the *packfor* package and retained the variables with a *P*-value < 0.05. Geographical distance and climate were excluded from RDA analyses and incorporated in forward selection in separate analyses, and further in variation partitioning. A permutation test was used to test for the significance of the axes eigenvalues associated with significant environmental variables. A permutational multivariate analysis of variance based on a Bray-Curtis distance matrix was used to assess significance of differences among ecoregions for overall species assemblages and environmental variables using the function *Adonis* of the *vegan* package.

A fourth-corner analysis (Dray & Legendre 2008) using the *ade4* package (Dray & Dufour 2007) was used to assess the relationship simultaneously between separate traits, species abundance and environmental/climatic variables. Missing entries of the categorical traits were replaced by predicted values using *imputMCA* function of the *MissMDA* package (Josse & Husson 2016). Associations between categorical traits and quantitative environmental variables were measured by Pearson correlation coefficient. The significance was tested by a combination of the permutation model 2 and 4 with 999 permutations to obtain a correct level of Type I error.

3.4.2. Phylogeny reconstruction

Hypothesized molecular phylogenies of Diptera species from peatland sites were generated, one with the total species pool and three phylogenies comprising the local species pool of each

ecoregion. The DNA barcode (658 base pairs of the mitochondrial CO1-5P gene) was used as a proxy for species-level phylogenetic relationships (Joly et al. 2014). A compilation of published molecular sequences in the Barcode of Life Data Systems (BOLD) (Ratnasingham and Hebert 2007) and our own Diptera species representing 356 specimens and 139 species submitted to the Canadian Centre for DNA Barcoding for sequencing using C_LepFolF/C_LepFolR primers (Hernández-Triana et al. 2014) were used in a matrix of DNA sequences constructed with Mesquite 3.04 (Maddison & Maddison 2015) and aligned with MUSCLE (Edgar 2004). A Bayesian approach was used for the phylogenetic analyses using BEAST v1.7.5 (Drummond et al. 2012) and the output was examined via Tracer v.1.6 (Rambaut *et al.* 2014). To determine which model of nucleotide substitution best fit the alignment, JModeltest2 according to AIC criterion was applied. We constrained monophyly for families, sub-families, genera and groups for which there were recent and well-supported, multi-gene or morphological phylogenies. These included: Schizophora and some higher groups of acalyptrate Diptera (Yeates & Wiegmann 2005); Calyptratae (Lambkin et al. 2013); Sarcophagidae (Kutty et al. 2010, Pape, Blagoderov & Mostovski 2011); *Ravinia* (Sarcophagidae) (Giroux, Pape & Wheeler 2010, Piwczynski et al. 2014); *Boettcheria* (Sarcophagidae) (Piwczynski et al. 2014); Luciliinae and Polleniinae (Calliphoridae) (Kutty et al. 2010); Phytomyzinae (Agromyzidae) (Scheffer et al. 2007); Scathophagidae (Bernasconi et al. 2000); Milichiidae (Brake 2000); Sciomyzidae, Sciomyzini, Tetanocerini (Tóthová et al. 2013); Tephritidae (Han & Ro 2009); Drosophilidae (Yassin 2013); Chloropinae (Chloropidae) (Brake 2000). Sequences of *Dolichopus brevipennis* (Dolichopodidae), *Sphaerophoria philanthus* (Syrphidae), *Chelipoda truncata* (Empididae), *Hypocera ehrmanni* (Phoridae), *Lonchoptera furcata* (Lonchopteridae) were used to root the tree (outgroup).

The GTR+I+G model was selected as the appropriate model by JModelTest2 and no partitioning by codon was used. In all analyses, strong priors were set on the age of two nodes corresponding to Schizophora (LogNormal: Mean = 3, St. Dev. = 0.78, offset = 70) and Chloropidae (LogNormal: Mean = 3, St. Dev. = 0.7, offset = 42) according to paleontological and molecular data (Nardi et al. 2010, Wiegmann et al. 2011). A branching prior was set under a Yule process model and a relaxed molecular clock was assumed using a logNormal distribution of rates (Drummond et al. 2006). The analyses were performed twice for each phylogeny using a random

starting tree for a MCMC chain length of 40 million generations (10000 echo states, 4000 log parameters, 20% burn-in). The exception was the Saguenay phylogeny which used a chain length of 100 million generations (10000 echo states, 1000 log parameters, 20% burn-in) to produce an adequate effective sample size.

3.4.3. Phylogenetic community structure

The phylogenetic structure was first calculated for all Diptera pooled in each trap and repeated at each higher spatial scale: for each site and in each ecoregion. To determine if Diptera communities are more or less related than expected by chance several indices were calculated. Faith's phylogenetic diversity metric (PD) (Faith 1992) was calculated for each community. The mean pairwise distance (MPD), calculated as the mean phylogenetic distance among all pairwise combinations of co-occurring species and the mean nearest taxon distance (MNTD) were calculated as the mean phylogenetic distance to most closely related species for all co-occurring species (Webb 2000, Webb, Ackerly & Kembel 2008). A null model shuffling taxa labels to generate null communities randomized 999 times was used to determine if the phylogenetic composition of communities differed significantly from that expected by chance. These 999 null measurements were used to calculate two measures of standardized effect size multiplied by -1: Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) (observed value minus the mean value of the 999 null values divided by the standard deviation of the 999 null values) and probabilities. To estimate whether NTI and NRI values at the trap and site scales were significantly different from zero, t-tests were performed. Fisher's combined probability tests were performed as meta-analyses of *P*-values using *sumlog* of the *metap* package (Dewey 2016). Null models were used at the ecoregion scale to assess if communities were significantly different from random.

3.4.4. Phylogenetic signals in trait diversity

The phylogenetic signal is defined as the tendency for related species to resemble each other. Trait conservatism is related to a higher degree of phylogenetic signal, meaning that close relatives share similar traits, while trait convergence is the tendency for distantly related species to resemble each other more than expected (Blomberg et al. 2003). Phylogenetic signals of continuous traits were tested with Blomberg's *K* and for significance we randomly arrayed the

trait data on the community phylogeny 999 times to generate a null distribution from which a *P*-value could be calculated using the *picante* package. Phylogenetic signals of categorical traits were measured using Pagel's lambda with the *fitDiscrete* function in the *Geiger* package (Harmon et al. 2008). By comparing the likelihood ratio test of a model where the tree is transformed by lambda and one where the tree is transformed into a large polytomy ($\lambda = 0$), we can predict which one fits better by a chi-square distribution.

To evaluate the variation of alpha diversity along anthropogenically modified landscapes, a series of linear models were used to evaluate linear relationships among measures of Abun, S, Srare, Chao1, FRic, FDiv, FEve, NRI and NTI to the proportion of anthropogenically modified land (urban development + agriculture).

To evaluate the phylogenetic turnover in Diptera communities within and between the three ecoregions, beta phylogenetic differences were tested using *comdist* (betaMPD: the average MPD for each species in a sample to all species in another sample) and *comdistnt* (betaMNTD: the average MNTD for all species in a sample to the nearest neighbors in another sample) functions of the *picante* package. Then PCoA of the output dissimilarity matrix was computed, and principal coordinates eigenvalues were used as response variables in RDA to determine the effect of environment on betaphylogenetic structure. To determine if beta and phylobeta diversity were positively spatially autocorrelated, the Mantel statistic was calculated with spatial distance. To assess correlations between species co-occurrence and phylogenetic distances, the Mantel statistic was also performed between Bray-Curtis dissimilarity matrices and betaphylogenetic dissimilarity matrices.

Variation partitioning was used to assess the proportion of variation in betadiversity explained by environmental, spatial and climatic variables at the taxonomic, functional and phylogenetic levels. The variation was partitioned into several components depending on significance according to forward selection: pure environmental component (local and surrounding variables), pure climatic component, pure spatial component, spatially structured environmental and/or climatic components and residual variation. ANOVA was used to calculate the significance levels of the different components. These analyses were computed with the *vegan* package.

3.5. RESULTS

3.5.1. Species and functional alpha and beta diversity

A total of 3302 specimens belonging to 202 species in 21 families was identified from the 15 bog sites in the three ecoregions (Appendix 3.1). Neither abundance, observed species richness, rarefied species richness nor Chao1 indices were significantly different among and within the three ecoregions ($p > 0.05$), although there was a tendency for a decrease in diversity from south to north. The three functional indices FRic, FEve and FDiv were not significantly different among sites and between the three ecoregions ($p > 0.05$). Functional space occupied by species assemblages was low across all sites, functional evenness was moderately high and divergence was high (Table 3.2).

The community weighted means (CWM) (Table 3.3) showed that species inhabiting Montreal and Saguenay sites possessed similar traits, predominantly saprophagous generalist species preferring moist substrates for oviposition. The functional composition of James Bay sites was clearly separated from the other two ecoregions as communities were dominated by sapropagous and predacious species specialized on insect or arthropods that use terrestrial conditions for oviposition. Nearly all communities were dominated by widespread species found in at least six sites and in the three ecoregions; also species were adapted to a large temperature range and were wetland facultative. Several significant relationships among species functional traits and environment and climate were found by the fourth corner analysis (Figure 3.2). The saprophagous generalist species inhabiting Montreal and Saguenay bogs were positively influenced by the coverage of wetlands surrounding the sites, although the warm temperature negatively impacted them. Insect predators in James Bay bogs were positively influenced by the fluctuation in the level of water, longitude, forests surrounding the sites and tree cover within the sites. Habitat preference for oviposition, voltinism, size, frequency of occurrence and rarity were not significantly correlated with any measured environmental parameters.

The three ecoregions were significantly different (Adonis $R^2 = 0.47$, $p = 0.001$) in species assemblages. Climate was significantly different between the three ecoregion (Adonis $R^2 = 0.98$, $p = 0.001$), and the other environmental variables were significantly different between

ecoregions (Adonis $R^2 = 0.77$, $p = 0.001$) also. The total proportion of variance explained in species RDA by four explanatory variables (surrounding forests, pH, PC1, PC2) was 53 % (adjusted $R^2 = 0.34$) (Figure 3.3 A). Montreal species composition in RDA was mostly affected by higher pH, PC2 and PC1, while Saguenay species were not affected by precise environmental variables. James Bay species composition was primarily affected by surrounding forests and by higher coverage of bog specialist plant species *Maianthemum trifolium* and *Chamaedaphne calyculata* (PC1). Montreal and Saguenay ecoregions were not significantly different in functional composition (Adonis $R^2 = 0.98$, $p = 0.18$). Four different environmental variables (surrounding forests, area, PC2, PC4) emerged in RDA as having a significant effect on functional composition explaining 51 % (adjusted $R^2 = 0.39$) of variance (Figure 3.3 B). Large area predominantly affected functional composition of Montreal and Saguenay bog sites. Two Montreal sites that were dominated by specialist phytophagous species (CWM) were mostly affected by a high coverage of *Carex oligosperma* and low litter cover (PC2); and high coverage of *Polytrichum* spp. and low *Eriophorum vaginatum* subsp. *spissum* (PC4). James Bay communities were mostly affected by the high percentage of surrounding forest.

3.5.2. Phylogenetic alpha and beta composition

Using phylogenies constructed with the regional species pool and local species pools found similar results at all scales, with a few exceptions (Table 3.4). At the trap scale, mean PD was not significantly different from random for both local and regional phylogenies. Mean NTI were significantly more than 0 for Montreal and Saguenay for both phylogenies and the same results as NTI were found for mean NRI. At the site scale, mean PD was significantly different from 0 for Montreal and Saguenay communities for both phylogenies. Mean NTI of Montreal and Saguenay communities were significantly clustered with the regional phylogeny, although only Montreal was clustered with the local phylogenies. For mean NRI, Montreal communities were clustered with both phylogenies, although James Bay communities appeared clustered with the local phylogeny. At the ecoregion scale, PD was significantly different from null expectations for Saguenay with the regional phylogeny only. NTI was significantly clustered for Montreal with the regional phylogeny only. NRI was significantly clustered for Montreal only for both phylogenies. All other communities at the different scales not mentioned above were not significantly different from random. Mantel correlation between beta and phylobeta diversity

was significantly correlated to spatial distance for species ($r = 0.68$, $p = 0.001$), MNTD ($r = 0.53$, $p = 0.002$) and traits ($r = 0.43$, $p = 0.003$), although not MPD ($r = 0.001$, $p = 0.45$). Species co-occurrence was significantly correlated ($p < 0.05$) to phylogenetic distances and functional distances.

The three ecoregions were significantly different in phylobetadiversity (BetaMNTD Adonis $R^2 = 0.68$, $p = 0.001$; BetaMPD Adonis $R^2 = 0.38$, $p = 0.001$). The total variance explained by RDA in BetaMNTD by four explanatory variables was 31 % (adjusted $R^2 = 0.22$) (Fig. 3.4A).

Phylogenetic structure at the Montreal sites at the tip of the tree was mostly influenced by substrate coverage (PC1), while Saguenay communities were mainly affected by the large bog areas and substrate coverage (PC2) in this ecoregion. James Bay communities were affected by low vegetation surrounding the sites. The low total variance explained by RDA in BetaMPD by two explanatory variables was 19% (adjusted $R^2 = 0.06$) (Fig. 3.4B). Surrounding exposed lands were affecting the majority of Montreal communities, while surrounding forests were affecting James Bay communities. Forward selection analyses showed that overall BetaTD, BetaFD and BetaMNTD were significantly associated with geographical distances, while BetaMPD was only significantly associated with east-west coordinates. The variation partitioning analyses (Fig. 3.5) explained 45 % of the total variation of BetaTD with the shared spatial, environmental and climatic fraction explaining the highest proportion of variation (24 %, $p = 0.001$). Pure environmental variables accounted for 8 % ($p = 0.001$) of the variation, while climate accounted for 2 % (TempWarm, MaxTemp; $p = 0.001$). The shared component between environmental, spatial and climatic variables accounted for 18 % ($p = 0.003$) and the pure environmental fraction accounted for 14 % ($p = 0.002$) and climate accounted for 9 % (TempWarm, MaxTemp; $p = 0.001$) of the total variation (50 %) of BetaFD. The shared fraction of spatial, environmental and climatic (AnnuTemp, MaxTemp) variables explained 16 % ($p = 0.001$) of the total variation (26 %) of BetaMNTD. The shared spatial, environmental and climatic fraction explained the highest proportion of variation (4 %, $p = 0.001$) of the total variation (11 %, $p = 0.01$) in BetaMPD. The pure climatic distance (TempWarm, MaxTemp) explained only 0.7 % ($p = 0.001$) of the variation.

Linear models indicated that S was significantly positively related to agriculture ($df = 12$, $F = 3.29$, $R^2 \text{ adj} = 0.25$, $p = 0.04$). Urban development and agriculture had an additive effect on FDiv with a negative and positive association respectively ($df = 12$, $F = 8.73$, $R^2 \text{ adj} = 0.52$, $p = 0.005$). PD had a similar association with agriculture as S ($df = 12$, $F = 4.04$, $R^2 \text{ adj} = 0.30$, $p = 0.03$). NTI was positively related to urban development ($df = 12$, $F = 5.02$, $R^2 \text{ adj} = 0.36$, $p = 0.012$), so with increasing urban coverage, clustering is increasing.

The three ecoregions were significantly different in beta phylogenetic diversity (betaMNTD: Adonis $R^2 = 0.47$, $p = 0.001$; betaMPD: Adonis $R^2 = 0.47$, $p = 0.001$). Phylogenetic turnover was higher deeper in the phylogeny (betaMPD) for Montreal communities than within the other two ecoregions (Fig. 3.4 B).

Tests of phylogenetic signal showed that traits showing a signal are phylogenetically labile, with close-relatives less similar than expected under a Brownian model of evolution. The K statistic was significantly different than a signal expected by chance but less similar ($K < 1$) than expected under a Brownian model for Size ($K = 0.68$, $p = 0.001$) and Temp ($K = 0.29$, $p = 0.01$). Pagel's lambda was not significantly different ($p > 0.05$) from a giant polytomy for all other categorical traits.

3.6. DISCUSSION

The degree to which Diptera assemblages in bogs across different ecoregions are maintained by competition-driven differentiation, environmentally-filtered coexistence or stochasticity is more evident with the different predictions inferred from species co-occurrences, phylogenetic relatedness and functional structure. We did not find evidence of limiting similarity as a mechanism of Diptera community assembly in bogs at any spatial scale. Biotic interactions have been rarely considered important mechanisms controlling invertebrate species biodiversity in wet environments (Batzer & Wissinger 1996, Vinson & Hawkins 1998) and this still holds with the avenue of phylogenetic analyses (Ruhí et al. 2013, Grégoire Taillefer and Wheeler, Chapter 2). Results suggest that dispersal limitation, coupled with environmental filtering, caused by the strength of the environmental gradients is driving the spatial patterns observed in bog Diptera communities. Pangjanda & Pramual (2016) also found that black fly communities in streams

were randomly assembled, although in their study an equivalent proportion of communities showed clustering and overdispersion which led to overall randomness. In our study, an historical imprint caused by dispersal limitation over time likely created these phylogenetic random patterns (Hubbell 2001). This reasoning is consistent with findings in stream metacommunities; where abundant, small bodied, multivoltine insect species were affected by stochastic processes (Saito et al. 2015). These functional traits are similar to our dominant traits in every bog community; common species had small sizes, therefore they likely benefited from dispersal by wind (Kovats et al. 1996, Heino 2013) which explains their occurrence in the three ecoregions. However, with recent drastic human modification of the landscape, less suitable patches and more barriers to dispersal are found neighboring those bogs, so agriculture and urban development act as filters for the small proportion of species in the species pool that can disperse in these conditions. A selective filtering role of anthropogenic disturbances has been found for several other taxa (Brunbjerg et al. 2012, Ding et al. 2012, Concepción et al. 2016, Hausberger and Korb 2016, Mykrä et al. 2016).

As local variation in species diversity and composition are dependent on historical diversification and dispersion, a larger latitudinal gradient would have been necessary to detect a change in species diversity and an effect of species pools (Martin 2016). Here, assembly rules are mostly dictated by patch and landscape parameters affecting dispersal and establishment between sites. Contrary to our hypothesis, pure climatic variables were not the major determinants of community structure. Bog communities are distributed along broad environmental gradients in surrounding land-use and anthropogenic disturbance. Montreal bogs can be seen as more isolated systems, where exchange with the anthropogenically disturbed surrounding environment is difficult; on average 28 % of the proportion of the 2-km radius area around each bog was anthropogenetically modified. This is also illustrated by the higher variation in betaMPD (Fig. 3.4B) observed compared to the other two ecoregions. This is similar to Angold et al. (2006) who found that anthropogenic activities and urban environmental conditions influence species diversity and composition. Vegetation structure, the level of disturbance affecting the dominance of generalists and woodland specialists are the most significant influence on ground beetle (Coleoptera: Carabidae) assemblages in urban habitat patches. While Saguenay bogs are more intermediate (~ 5% of anthropogenic land-use, 36% forest, 43% wetlands) and James Bay bogs

are more open systems, where exchange can happen with the surrounding undisturbed environment (~ 0.03% of anthropogenic modification). Predacious insect species in James Bay immigrate from the surrounding forests as the bogs in this region are connected to a complex of forests (~ 80% land cover) and wetlands (~ 9% land cover). Consequently, community assembly within regions in unique habitats and low dispersal rates usually converge in phylogenetic clustering of assemblages, whereas in regions where dispersal is prevalent, assembly patterns should be largely stochastic and dominated by species dispersal capacity (Emerson & Gillespie 2008, Weiher et al. 2011).

High levels of functional divergence are associated with a high degree of niche differentiation among species within communities: the most abundant species are very dissimilar and compete weakly. As shown in the CWM analysis, common species were facultative wetland inhabitants and functional divergence was increasing with the coverage of agricultural land but decreasing with urban development. Consequently, the recent species turnover in Montreal must originate from species inhabiting surrounding agricultural land that possess very dissimilar traits to peatland inhabiting species. And as these peatlands possess unique features in an urban matrix, clustering at the tip of the phylogeny (NTI) is probably due to *in situ* environmental filtering (Fig. 3.4A: PC1 and PC2) and low dispersal rates of generalist saprophagous species from surrounding wetlands (Table 3.2). Another study encompassing more environmental heterogeneity in Montreal region (Grégoire Taillefer and Wheeler, Chapter 2) showed that bogs have harsher environmental conditions compared to other wetland types, which also act as selective pressure. Therefore, heterogenization of communities, functional richness and redundancy levels in bogs are systematically limited despite differences in species assemblages.

The large proportion of unexplained variation in beta diversity for each facet of biodiversity considered, suggests that other factors are determining community patterns. These factors are probably spatially structured environmental factors, such as a combination of local and surrounding conditions with dispersal limitation. Moreover, taxonomic turnover was high between ecoregions which increased phylogenetic turnover, and beta diversity was correlated with spatial distance except betaMPD, which was only affected by longitude. Soininen, McDonald & Hillebrand (2007) found in a meta-analysis that shifts in community composition

were happening at the scale of 1000 km in line with large scale variability in environmental conditions and that passive vs active dispersal did not have an effect on species turnover with increasing spatial scale. Here, BetaMPD might be correlated more to Pleistocene glaciations and Holocene post-glacial dispersal, as these had a profound impact on Nearctic biotas in a diversity of habitats (Lafontaine & Wood 1988, Harris & Taylor 2010, Solecki, Buddle & Wheeler 2016). Long-term dispersal limitation in an east-west direction, from coastal to more continental conditions, seems to shape the original betadiversity, as explained variation in betaMPD was mostly driven by pure spatial factors. Arnan, Cerdà & Retana (2015) found similar results for the three different facets of diversity in ant assemblages, spatial factors thus dispersal limitation played a major role in shaping ant communities in different climatic and human disturbed environments across Europe.

3.7. CONCLUSIONS

The major forces structuring Diptera assemblages in bogs across Quebec are stochastic processes, such as dispersal limitation of abundant, small, multivoltine species. Although, those random patterns change to environmental filtering with anthropogenic disturbances modifying the landscape. The massive Diptera radiation that began in the early Cenozoic and the different historical disturbances are at the origin of the functional and phylogenetic structure observed for peatland Diptera. Using only traditional metrics, it would not have been apparent that Montreal bog communities are impacted by land-use changes and that these impacts change the species pool capable of inhabiting these isolated unique habitats (Saito, Siqueira & Fonseca-Gessner 2015). This suggests that the three levels of diversity studied are complementary and give a different picture of macroecological patterns in those threatened habitats. Our results show that conservation of mobile organisms in bogs will depend on conservation plans focusing on both patch quality and surrounding landscape. Different conservations strategies need to be applied in the different ecoregions. Montreal should be prioritized for biodiversity conservation and unique roles of wetlands should be key factors to maintain high species richness. Residential developments affecting wetland habitats represent 64 % of permits emitted in Montreal by the Quebec Government, followed by industrial/commercial developments (Pellerin & Poulin 2013). Avoidance or minimization of direct and indirect impacts on area and values of wetlands should be the first mitigation measures recommended. Habitat corridors between wetland or forest

patches could mitigate the effect of habitat fragmentation, as the latter have been shown to influence both community and ecosystem function, such as nutrient fluxes (Tewksbury et al. 2002, Staddon et al. 2010). In Saguenay the large bog areas should be maintained as this diminishes the surrounding landscape pressure and with the continuing increase of human-induced changes, this will become more important. Horticultural peat extraction is increasing in this region and as in Montreal industrial/commercial developments are major threats. Mandatory compensatory mitigation should be applied such as restoration of functions and values after peat extraction and creation of new wetlands to replace wetland area and value if avoidance or minimization is not possible (Pellerin & Poulin 2013). Although, protection of natural wetlands is recommended as the functions and ecosystem services of restored or created wetlands are usually inferior to natural wetlands (Moreno-Mateos et al. 2012). Finally, protecting clusters of forest and wetlands in James Bay is a more effective conservation strategy than preserving islands of peatlands, as mobile organisms may see clusters of habitat as continuous potential niches instead of unreachable islands (Hatfield & LeBuhn 2007). Developing a standard approach and efficient techniques for large-scale biodiversity monitoring such as high-throughput DNA sequencing (Gibson et al. 2015) to assess efficacy of mitigation measures would be highly valuable.

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Table 3.1. Life-history and ecological traits considered in this study including categories, abbreviations and trait determination notes. Traits were assigned at the species level and adult stage except for feeding habits and specialization (larval stage).

Trait	Categories/ Determination
Larval feeding habits (Feeding)	Saprophagous (SA), Predator (PR), Parasite/parasitoid (PA), Phytophagous (PH)
Specialization (SpeGen)	Specialist (S) - feed on one genus/type of plant, animal or substrate, Generalist (G)
Size (mean of 2 specimens) (Size)	Small (<4 mm), medium (4–7 mm), large (>7 mm)
Voltinism (Voltinism)	Univoltine (U), Multivoltine (M) - ≥ 2 generations
Overwintering forms (Winter)	Egg (E), Larva (L), Pupa (P), Adult (A)
Habitat preference for oviposition (Oviposit)	Moist (M), Terrestrial (T), Lentic (L)
Preferred substrate (Substrate)	Carrion or dung (C), Detritus and microorganisms on soil (S), fungus, rotting wood, decaying vegetation (RW), Leaf litter (LL), Stem-borer (SB), Leaf-miner (LM), Flower consumer (FL), Insects or arthropods (I), Mammals, Amphibians (M), Secondary invaders (SI)
Wetland specialization (Wetland)	Obligate (O) - specialist found exclusively in wetlands, Amphibious (A) - at least part of their life cycle in wetlands and remainder in terrestrial

system, Facultative (F) - in terrestrial and wetland habitat, no life cycle restricted to water

Temperature range (Temp)

°C - determined using the difference between the maximum and minimum temperatures across sites in which the species was collected

Range (Range)

restricted (R): found in only one ecoregion; intermediate (I): found in two ecoregions; broad (B): found in three ecoregions

Frequency of occurrence
(Frequency)

1, rare (1 site); 2, infrequent (2 - 5 sites); 3, intermediate (6 - 10 sites); 4, widespread (11 - 15 sites)

Rarity (Rarity)

Rare < 18 specimens, Common \geq 18 specimens in total catch. For separation, an inflection point criterion was used from the rank abundance curve for the total abundance (Siqueira et al. 2012)

Table 3.2. Abundance (Abun), observed species richness (S), Chao1 indices (Chao1), rarefied species richness (Srare), functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) for all sites and mean diversity for each ecoregion. Site codes: MTL, Montreal (Eastern Canadian Forest); SAG, Saguenay (Eastern Great Lakes Lowland Forest) and BJM, James Bay (Central Canadian Shield).

Site	Abun	Mean		Mean		Mean		FRic	FEve	FDiv
		S	S	Chao1	Chao1	Srare	Srare			
MTL1	223	31		61.3		22.3		0.16	0.61	0.87
MTL2	165	40		55.5		31.0		0.31	0.71	0.84
MTL3	282	65	49	86.7	81	39.5	32	0.38	0.74	0.93
MTL4	459	70		136.1		31.0		0.54	0.72	0.67
MTL5	101	38		66.9		38.0		0.21	0.73	0.74
SAG1	163	38		68.6		30.3		0.50	0.66	0.87
SAG2	150	42		57.0		35.9		0.30	0.73	0.79
SAG3	228	52	39	69.0	57	37.2	30	0.35	0.76	0.71
SAG4	268	32		47.2		20.1		0.22	0.67	0.65
SAG5	116	28		43.6		26.3		0.23	0.74	0.90
BJM1	256	38		72.2		24.2		0.41	0.68	0.92
BJM2	208	38		72.0		27.9		0.30	0.65	0.84
BJM3	161	34	35	43.1	55	27.4	24	0.48	0.76	0.91
BJM4	308	33		44.4		19.1		0.39	0.69	0.78
BJM5	214	33		46.0		23.1		0.25	0.74	0.87

Table 3.3. Dominant functional composition of each site, represented by community-level weighted means (CWM). For continuous traits the mean trait value is weighted by abundance, while for categorical traits the dominant class is returned. For description of traits and associated codes refer to table 3.1.

	Feeding	Size	SpeGen	Oviposit	Substrate	Range	Frequency	Rarity	Temp	Voltinism	Winter	Wetland
MTL1	PH	2.2	S	M	SI	3	3	C	52.0	M	L	F
MTL2	PH	2.8	S	M	SB	3	4	C	52.0	M	L	F
MTL3	SA	3.6	G	T	SI	3	3	C	50.9	M	L	F
MTL4	SA	2.8	G	M	RW	1	2	C	50.6	M	A	F
MTL5	SA	2.9	G	M	I	3	4	C	52.3	M	P	F
SAG1	SA	4.2	G	M	I	3	3	C	52.9	M	L	F
SAG2	SA	4.0	G	M	C	3	3	C	51.8	M	P	F
SAG3	SA	4.6	G	T	C	3	3	C	52.5	M	P	F
SAG4	SA	3.2	G	M	I	3	3	C	51.4	M	P	F
SAG5	SA	4.0	G	M	SB	3	3	C	53.1	M	L	O
BJM1	PR	2.4	S	T	I	3	3	C	51.2	M	A	F
BJM2	SA	2.8	S	T	I	3	3	C	52.6	M	A	F
BJM3	SA	4.1	S	T	I	3	3	C	52.3	M	A	F
BJM4	PR	2.6	S	T	I	3	3	C	53.1	M	A	F
BJM5	PR	3.0	S	T	I	3	3	C	53.0	M	A	F

Table 3.4. Phylogenetic diversity (PD), net relatedness index (NRI) and nearest taxon index (NTI) for Diptera communities in 15 sites across three ecoregions at three spatial scales (trap, site, ecoregion). Fisher’s combined probability tests were performed to assess if overall *P*-values were significant at the trap and site scales. Null models were used at the ecoregion scale to assess if communities were significantly different from random. Significant *P*-values are in bold font.

		PD	<i>P</i> -value	NRI	<i>P</i> -value	NTI	<i>P</i> -value
Regional phylogeny							
Trap_{mean}	MTL	381	0.46	0.43	0.01	0.35	0.02
	SAG	367	0.01	0.98	< 0.001	0.80	< 0.001
	BJM	293	0.17	0.77	0.10	0.76	0.07
Site_{mean}	MTL	2132	< 0.001	1.29	0.01	1.53	< 0.001
	SAG	1576	< 0.001	0.40	0.17	0.80	0.02
	BJM	1548	0.38	0.81	0.06	0.22	0.51
Ecoregion	MTL	4794	0.42	2.25	0.03	1.64	0.04
	SAG	2856	0.002	-0.22	0.52	1.40	0.09
	BJM	2950	0.61	0.90	0.15	-0.21	0.58
Local phylogenies							
Trap_{mean}	MTL	378	0.19	0.36	0.01	0.35	0.02
	SAG	366	0.09	0.73	< 0.001	0.60	< 0.001
	BJM	304	0.16	0.79	0.10	0.75	0.07
Site_{mean}	MTL	2082	< 0.001	1.94	0.003	1.63	0.001
	SAG	1546	0.03	-0.18	0.71	0.20	0.32
	BJM	1505	0.06	1.73	0.003	0.63	0.18
Ecoregion	MTL	4601	0.07	2.76	0.02	1.39	0.09
	SAG	2796	0.50	0	0.45	0.61	0.28
	BJM	2809	0.33	2.17	0.05	0.51	0.31



Figure 3.1. Map of the 15 study peatland sites across Quebec, Canada. Map is separated into ecoregions: Montreal - Eastern Great Lakes Lowland Forest; Saguenay - Eastern Canadian Forest; James Bay - Central Canadian Shield (Ricketts and Himhoff 2003). Map created with SimpleMappr (www.simplemappr.net).

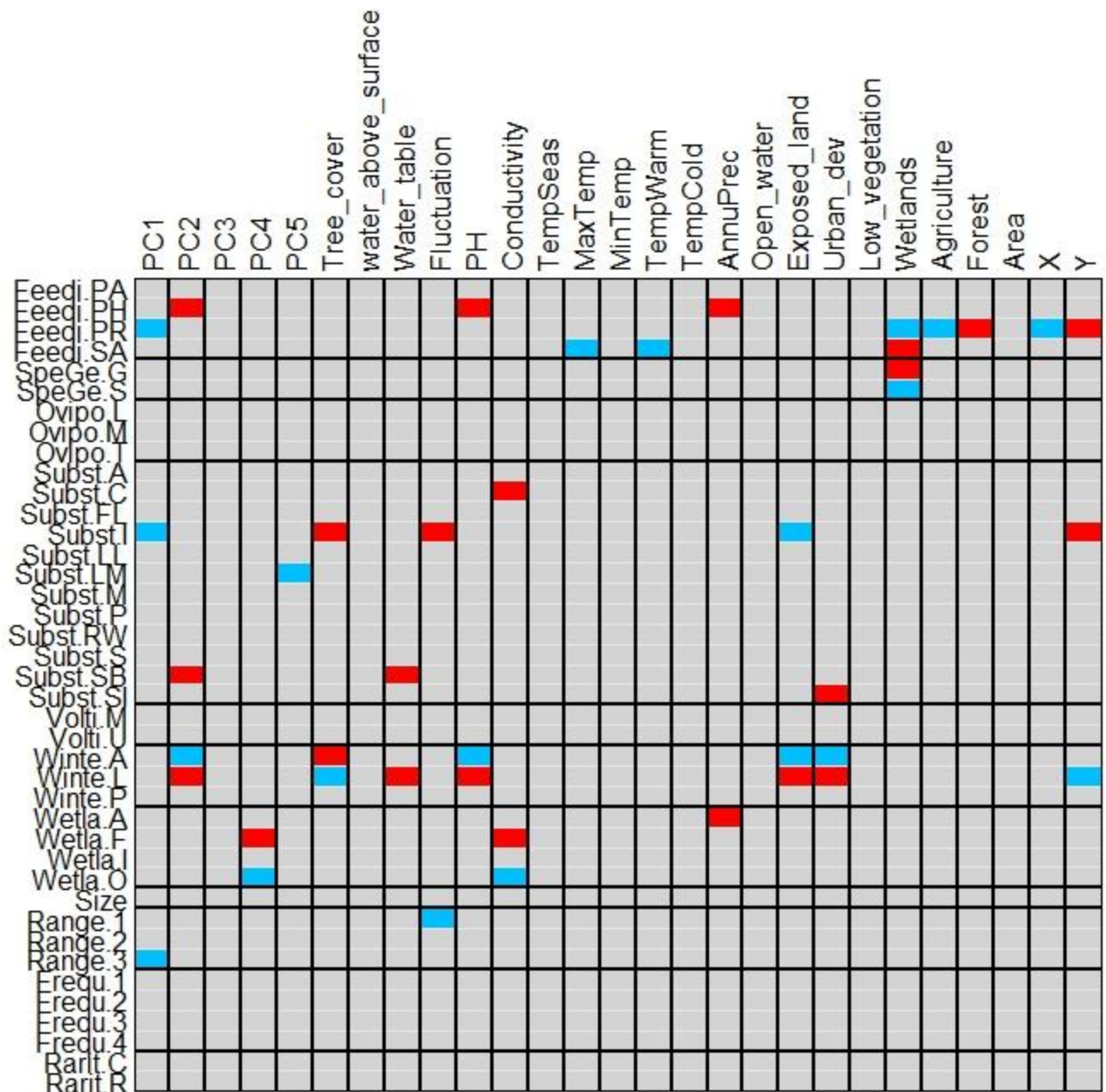


Figure 3.2. Relationships between Diptera species functional traits and environmental/climatic variables revealed by fourth-corner analysis. Blue cells correspond to negative significant relationships; red cells correspond to positive significant relationships.

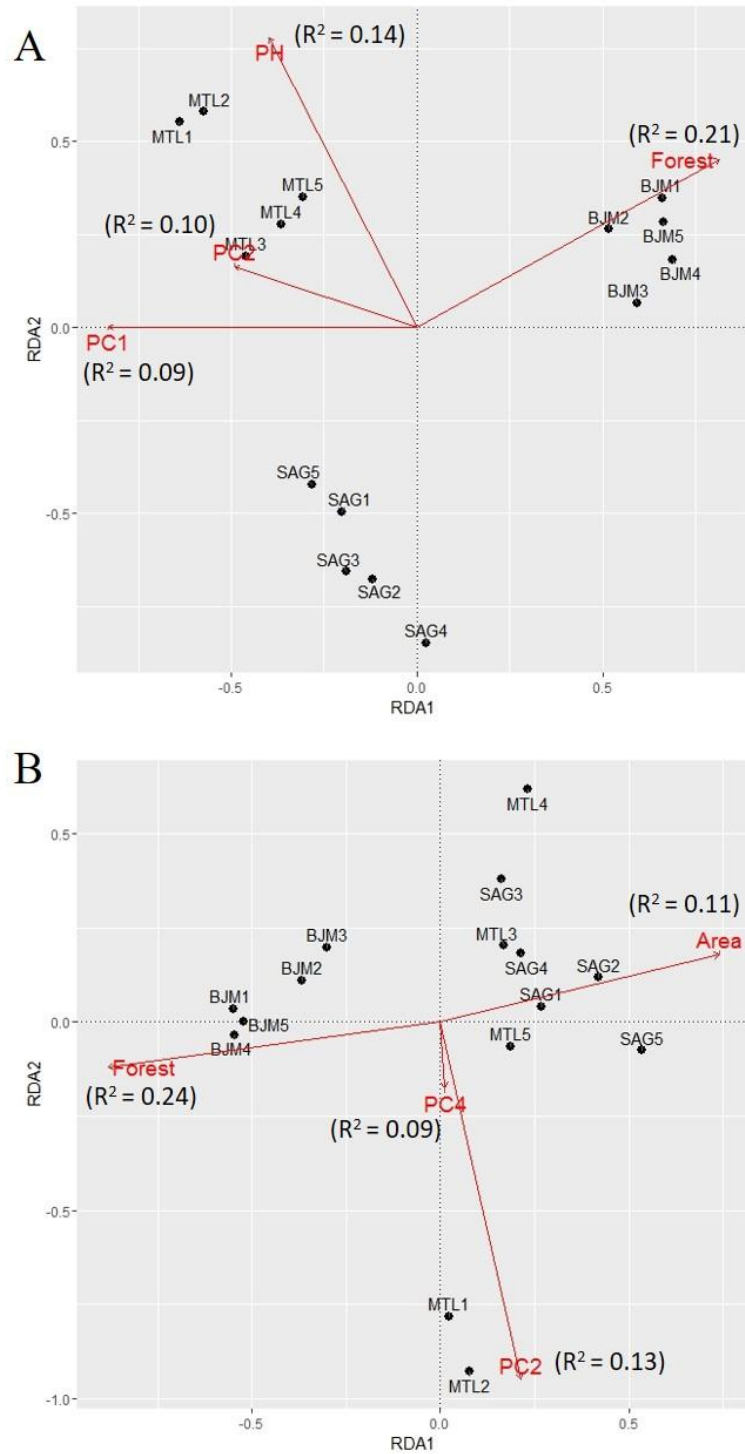


Figure 3.3. Redundancy analyses of species (A) and functional composition (B). Arrows represent vectors of significant variables ($p < 0.05$) explaining community structure, R-squared values in parentheses from the forward-selected models examining the effect of environmental factors.

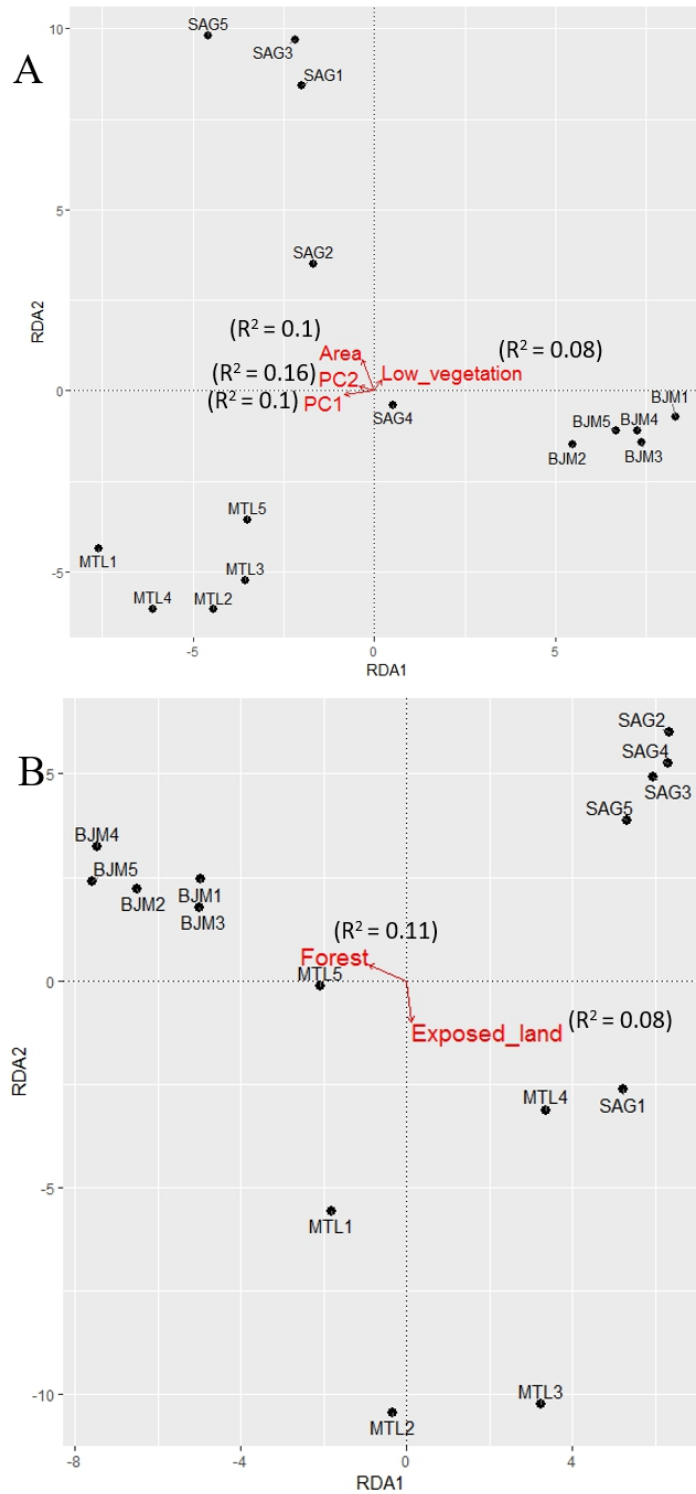


Figure 3.4. Redundancy analyses of beta phylogenetic composition for mean nearest taxon distance MNTD (A) and mean pair-wise distance MPD (B). Arrows represent vectors of significant variables ($p < 0.05$) explaining community structure, R-squared values in parentheses from the forward-selected models examining the effect of environmental factors.

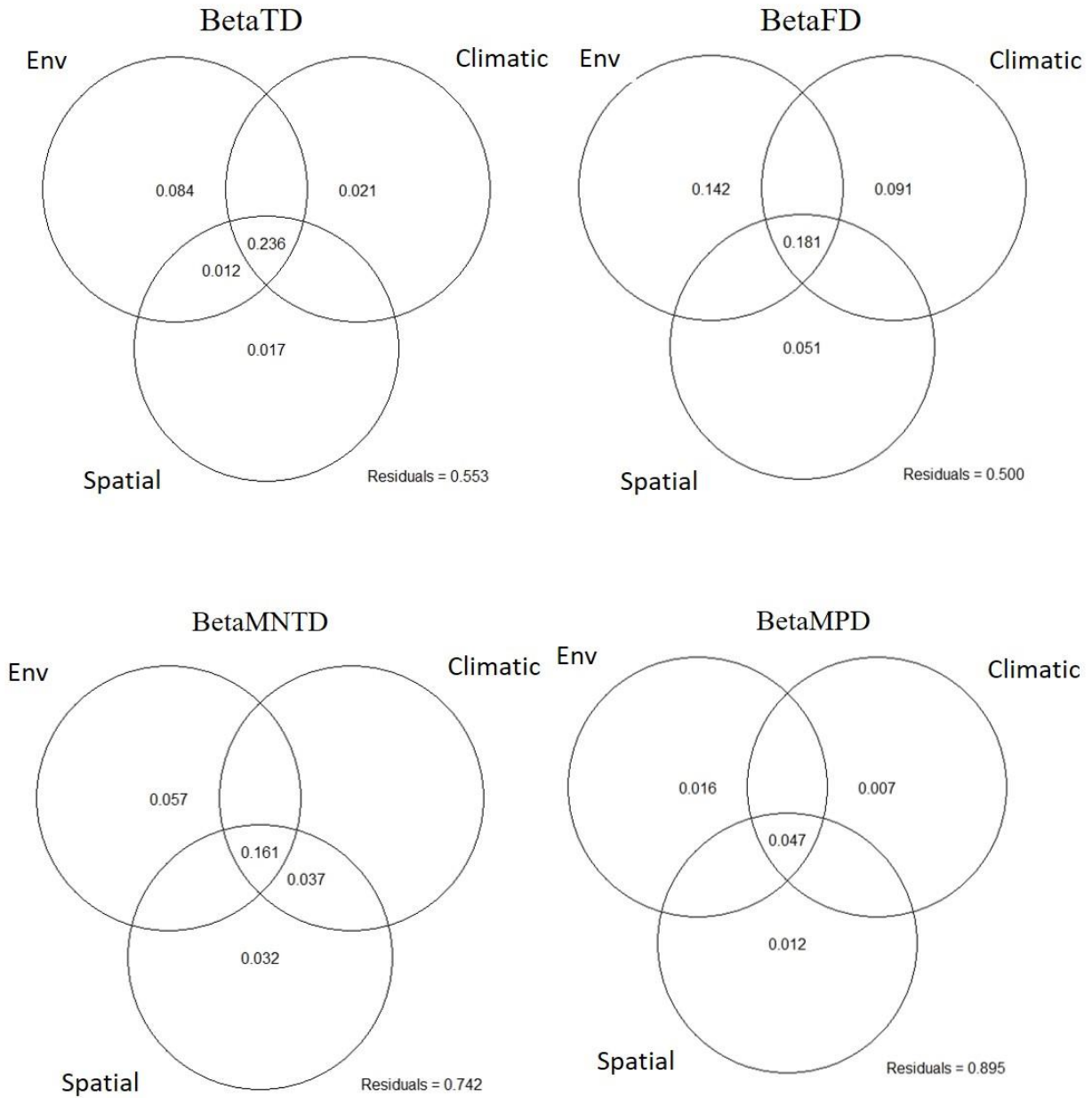


Figure 3.5. Variation partitioning diagrams of taxonomic (BetaTD), functional (BetaFD) and phylogenetic (BetaMNTD, BetaMPD) composition. Circles represent variation explained by unique and shared fractions of significant (based on forward selection) environmental, climatic and spatial variables, while numbers correspond to the adjusted coefficient of determination (adjusted R^2) associated to each circle. Only significant and positive adjusted R^2 are shown.

CHAPTER 4: General discussion, conclusion and future directions

4.1. INTRODUCTION

Community structure and spatial distribution of species are fundamental fields in ecology, evolution and conservation biology. There is an increasing need to examine spatially distinct areas for multiple taxonomic groups at multiple spatial scales to gain new perspectives on how communities assemble, and change over time. To investigate the effect of wetland type, space and human-induced changes on faunal communities, I applied a multidisciplinary approach comparing taxonomic, functional and phylogenetic patterns. The choice of Diptera as a study taxon was enhanced by their high abundance and species richness in wetlands, great diversity of feeding habits, short generation time, high reproductive capacity and wide range of ecological specialisation across species.

4.2. SUMMARY OF RESEARCH

4.2.1. Phylogenetic and taxonomic responses of Diptera communities to wetland habitats

In Chapter 2, my objectives were to describe taxonomic, functional and phylogenetic structure in three classes of wetlands (bogs, swamps, marshes) in a 60 km radius around Montreal, Quebec. Also, I wanted to assess if rarity is deterministic or essentially stochastic and how beta- and phylobeta- diversity are related to environmental conditions. Twenty-eight Diptera families representing 295 species with a range of functional characteristics were identified from 12 wetland sites. I compared taxonomic diversity indices across the three classes of wetlands as well as phylogenetic relationship indices and used ordinations to visualize community structure and relationships to environmental variables. Phylogenetic signal was measured for every species trait measured. I found that the three wetland types were similar in abundance, species richness and in overall functional composition of Diptera. However, the different wetland types supported distinct species assemblages and phylogenetic structure. Phylogenetic clustering tree-wide was observed for bogs, while a balance of clustering at the tip of the phylogeny and random phylogenetic distribution was observed for marshes. Swamps supported only random Diptera assemblages. These findings are consistent with an increase in clustering, thus environmental filtering, with environmental extremes. Rare species tended to be distantly related to common

species as a phylogenetic signal was found and were filtered by the environment. The three levels of betadiversity were significantly related to similar environmental variables, mainly local factors. Therefore, integrating taxonomic and functional responses with phylogenetic relatedness provided additional and complementary information about mechanisms driving biodiversity patterns.

4.2.2. Spatial patterns of taxonomic, functional and phylogenetic structure in peatlands

In Chapter 3, the objectives were to describe spatial distribution of Diptera across bogs in three ecoregions using three facets of biodiversity: taxonomic, functional and phylogenetic. I examined 202 species from 21 families of Diptera collected from 15 bog sites that spanned an anthropogenic disturbance gradient in Quebec. I included more functional traits than in Chapter 2 and calculated multi-dimensional trait metrics and phylogenetic signal indices. Redundancy analysis, variation partitioning, linear regression and phylogenetic community metrics were used to determine the biodiversity patterns and the environmental variables influencing them. The three ecoregions supported similar abundance, species richness and functional diversity. Although each ecoregion had a different community composition and did not share evolutionary history even though some small, common species were able to colonize the three ecoregions probably through wind dispersal over a long period of time. Patterns of species occurrence were correlated with stochastic processes and the environmental conditions at and surrounding each bog sites. Open and more topographically homogeneous settings as for Saguenay and James Bay bogs are promoting random assemblages with species immigrating from surrounding forests and wetlands. Human-induced changes in Montreal increased selective pressure on Diptera communities and increased phylogenetic clustering.

4.3. SYNTHESIS AND RECOMMENDATIONS FOR FUTURE WORK

In Chapter 2, more habitat heterogeneity was encompassed in a human dominated landscape context and a larger species pool was used for phylogenetic analyses, therefore the species found in bogs are a small proportion of the species available to colonize that clustered in the phylogenetic tree. This suggests that bogs exhibit harsher environmental conditions than other wetlands. In Chapter 3, the larger spatial extent studied suggests that species are distributed in bogs not only by local niche-based processes, but also by the strength of the surrounding

environmental gradients and neutral processes. Competition driven patterns were not found in any type of wetlands, probably because species were sorted solely as a function of the harsher and unique environmental conditions in wetlands, where species possessing certain traits enabling them to survive these conditions can establish. Moreover, weekly turnover of species with similar traits permit the high species richness. This study advances our understanding of how and what influence species distribution at different spatial scales as multiple taxa with a range of dispersal abilities and functional roles were used. Many authors share the view that communities are influenced simultaneously by both niche-based and neutral processes, as environmental conditions and dispersal limitation affect communities (Tilman 2004, Gravel et al. 2006, Holyoak and Loreau 2006, Jabot et al. 2008). We can probably change our view of two extreme models, either niche-related or neutral models, to a continuum where the position of the community would depend on the characteristics of the organisms and the spatial scales.

Given the rapid disappearance of wetlands and their invaluable roles for carbon sequestration, habitat for endangered species, water quality and supply; conservation and restoration concerns are rising. So to conserve habitat integrity and ecosystem roles it is imperative to know what is affecting the composition of species inhabiting those sites. The results of these two studies suggest that, when possible, conserving a matrix of forest and wetlands surrounding the bogs, as in James Bay, will maintain the roles and community structure in those habitats. Also, protecting a peatland area large enough that the surrounding land use does not have an effect, as in Saguenay, is an action that will conserve the integrity of bog ecosystems. When these wetlands are already set in an anthropogenically altered context, as in Montreal, attention should be directed to managing a forest buffer between agricultural lands and urban developments or developing a network of corridors to increase connectivity.

More efforts must be made to describe natural history, taxonomy, and ecology of Diptera species (Bortolus 2008) and produce more resolved phylogenies of groups of Acalypterae (Yeates et al. 2007). Diptera are found in virtually every environment with high diversity and is one of the most functionally diverse groups of organisms. As such, it has enormous potential for use as a model taxon in conservation studies to have a rapid understanding of diversity, ecology, and function in a particular habitat. Also, compiling and making freely available robust datasets and

identification tools for multiple taxonomic groups increases the effectiveness in capturing patterns of change in species composition across large regions (Cardoso et al 2011, Joly et al. 2014). As shown in these studies, using the three facets of biodiversity provides a comprehensive insight into how biodiversity is influenced by environmental gradients and changes. With the never ending human-induced perturbations to the environment, greater effort must be made to generalize statements about large-scale biodiversity patterns to be able to address problems in an efficient and timely manner.

This study is one of the most comprehensive datasets of Diptera diversity, functional traits and community composition of wetlands in Canada. These data, the voucher specimens deposited in a museum, and DNA sequences extracted will have continued use for future taxonomic and systematic studies, biodiversity assessments, community phylogenetic research, climate change influences and meta-analyses.

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5. APPENDICES: Supplementary materials for Chapter 2 and 3

Appendix 2.1. Traits assigned to each Schizophora species and morphospecies collected from each of the 12 wetland sites. Species in grey were excluded from analyses. (NA = unknown)

1. Larval feeding habit (Feeding) – SA: saprophage, PR: predator, PA: parasite/parasitoid, PH : phytophage
2. Size – mean of 2 specimens in mm (small (<4 mm), medium (4-7 mm), large (>7 mm))
3. Specialist/ Generalist (Spe/Gen) – S: feed on one genus/type of plant, animal or substrate, G
4. Habitat preference for oviposition (Habitat pref) – M: moist, L: lentic, T: terrestrial
5. Restriction to a wetland habitat (Type wetland) – R: restricted (found in only one wetland type), I: intermediate (found in two wetland types), B: broad (found in three wetland types)
6. Frequency of occurrence (Freq occurrence) – 1: only found in one site, 2: found in 2 to 6 sites, 3: found in 7 to 13 sites, 4: found in 14 to 16 sites.
7. Number of specimens collected (No specimens) – R: rare < 0.6% of total catch, C: common \geq 0.6% of catch
8. Voltinism – U: univoltine, M: bivoltine/ multivoltine.
9. Overwintering stage (Overwin stage) – E: eggs, L: larvae, P: pupae, A: adults.
10. Specialization (Specializ) – O: obligate (specialist found exclusively in wetlands), A: amphibious (at least part of their life cycle in wetlands and remainder in terrestrial system), F: facultative (occasionally found in wetlands for water or food)

Species	Feeding	Size	Spe/Gen	Habitat pref	Type wetland	Freq occurrence	No specimens	Voltinism	Overwin stage	Specializ
Micropezidae										
<i>Compsobata (Compsobata) sp.</i>	SA	7.33	NA	M	R	1	R	NA	NA	A
<i>Rainieria antennaepes (Say)</i>	SA	7.33	G	M	R	1	R	NA	NA	A
Lonchaeidae										
<i>Lonchaea sp.</i>	NA	3.53	NA	NA	I	2	R	NA	NA	NA
Pallopteridae										
<i>Temnosira subarcuata Johnson</i>	SA	4.47	NA	T	R	1	R	NA	NA	NA
Platystomatidae										
<i>Riviella pallida Loew</i>	PH	3.73	NA	NA	R	2	R	U	NA	NA
<i>Riviella sp.1</i>	PH	4.27	NA	NA	R	2	R	NA	NA	NA
<i>Riviella sp.2</i>	PH	4.63	NA	NA	I	2	R	NA	NA	NA
<i>Riviella steyskali Namba</i>	PH	4.60	NA	NA	R	1	R	NA	NA	NA
<i>Riviella variabilis Loew</i>	PH	5.77	NA	NA	I	2	R	NA	NA	NA

Tephritidae										
<i>Euaresta bella</i> (Loew)	PH	3.03	S	L	B	3	C	U	A	F
<i>Euleia fratria</i> (Loew)	PH	4.13	S	L	R	1	R	U	A	F
<i>Ictericia seriata</i> (Loew)	PH	4.67	S	L	R	1	R	U	A	F
<i>Paroxyna albiceps</i> (Loew)	PH	2.73	S	L	R	1	R	U	A	F
<i>Rhagoletis pomonella</i> (Walsh)	PH	3.47	S	L	R	1	R	U	A	F
<i>Urophora quadrifasciata</i> (Meigen)	PH	2.80	S	L	R	1	R	M	L	F
Ulidiidae										
<i>Chaetopsis fulvivrons</i> (Macquart)	SA	3.67	G	T	R	2	R	U	L	F
<i>Chaetopsis massyla</i> (Walker)	SA	4.70	G	T	I	2	R	U	L	F
<i>Euxesta notata</i> Wiedemann	SA	4.20	G	T	I	2	R	U	L	F
<i>Meliera similis</i> (Loew)	SA	5.43	NA	T	R	1	R	U	L	F
Chamaemyiidae										
<i>Leucopis americana</i> Malloch	PR	2.53	G	T	R	1	R	M	P	F
<i>Leucopis</i> sp.	PR	1.80	G	T	R	1	R	M	P	F
Lauxaniidae										
<i>Camptoprosopa</i> sp.	SA	3.33	G	M	R	1	R	NA	NA	NA
<i>Homoneura (Homoneura) incerta</i> (Malloch)	SA	3.10	G	L	R	1	R	U	L	F
<i>Homoneura (Homoneura) pernotata</i> (Malloch)	SA	3.87	G	L	I	2	R	M	L	F
<i>Homoneura (Homoneura) philadelphica</i> (Macquart)	SA	4.17	G	L	I	2	R	M	L	F
<i>Homoneura (Homoneura) ♀♀aequalis</i> group										
<i>Homoneura (Tarsohomoneura) americana</i> (Wiedemann)	SA	3.67	G	L	R	1	R	M	L	F
<i>Homoneura (Tarsohomoneura) houghii</i> (Coquillett)	SA	3.27	G	M	R	2	R	M	L	NA
<i>Homoneura (Tarsohomoneura) sheldoni</i> (Coquillett)	SA	3.07	G	M	I	2	C	M	L	O
<i>Lauxania shewelli</i> Perusse & Wheeler	SA	4.05	G	L	R	1	R	U	P	F
<i>Minettia (Minettia) cana</i> Melander	SA	3.40	G	M	R	1	R	U	P	F
<i>Minettia (Minettia) lupulina</i> Fabricius	SA	3.60	G	M	R	2	R	U	P	F
<i>Minettia lyraformis</i> Shewell	SA	4.00	G	M	R	1	R	U	P	F
<i>Poecilolycia aspinosa</i> Shewell	SA	2.87	G	M	R	1	R	NA	P	F
<i>Poecilolycia browni</i> Curran	SA	3.60	G	M	B	2	R	NA	P	F
Dryomyzidae										
<i>Dryomyza anilis</i> Fallén	SA	6.92	G	M	B	2	R	NA	NA	F
Sciomyzidae										
<i>Dictya</i> ♀♀spp.										

<i>Dictya expansa</i> Steyskal	PR	5.83	S	L	I	2	R	M	P	O
<i>Ditya pictipes</i> (Loew)	PR	5.87	S	L	R	1	R	M	P	O
<i>Elgiva sollicita</i> (Harris)	PR	6.87	S	L	R	1	R	M	A	O
<i>Limnia boscii</i> (Robineau-Desvoidy)	PR	5.43	S	T	B	2	R	NA	NA	A
<i>Limnia conica</i> Steyskal	PR	4.00	S	L	R	1	R	NA	NA	O
<i>Pherbecta limenitis</i> Steyskal	PR	5.23	S	L	R	1	R	NA	NA	O
<i>Pherbellia anubis</i> Knutson	PR	5.33	S	L	I	2	C	M	P	O
<i>Pherbellia griseola</i> (Fallén)	PA	4.17	G	T	R	1	R	U	E	F
<i>Pherbellia nana nana</i> (Fallén)	PA	3.00	G	T	R	1	R	U	E	F
<i>Pherbellia quadrata</i> Steyskal	PA	5.67	G	T	R	1	R	U	E	F
<i>Pherbellia vitalis</i> (Cresson)	PA	4.23	G	T	I	2	R	U	E	F
<i>Poecilographa decora</i> (Loew)	PR	5.53	S	L	R	1	R	NA	NA	O
<i>Pteromicra pectorosa</i> (Hendel)	PA	3.80	G	T	R	1	R	M	P	O
<i>Pteromicra similis</i> Steyskal	PA	4.50	G	T	I	2	R	M	P	O
<i>Sciomyza varia</i> (Coquillett)	PA	5.37	S	T	R	2	R	M	P	O
<i>Sepedon fuscipennis nobilis</i> Orth	PR	7.30	S	L	I	2	R	M	A	O
<i>Sepedon gracilicornis</i> Orth	PR	7.73	S	L	I	2	R	M	A	O
<i>Sepedon tenuicornis</i> Cresson	PR	7.60	S	L	R	1	R	M	A	O
<i>Tetanocera annae</i> Steyskal	PR	9.17	S	L	I	2	R	M	P	O
<i>Tetanocera fuscineris</i> Zetterstedt	PR	5.63	S	L	R	1	R	M	P	O
<i>Tetanocera plebeja</i> Loew	PR	7.92	S	L	I	2	R	M	P	O
<i>Tetanocera plumosa</i> Loew	PR	9.38	S	L	R	2	R	U	L	O
<i>Tetanocera rotundicornis</i> Loew	PA	7.77	S	T	R	1	R	M	P	O
<i>Tetanocera</i> sp.	PR	6.42	S	L	R	1	R	M	P	O
<i>Tetanocera valida</i> Loew	PR	7.50	S	L	I	2	R	M	P	O
<i>Trypetoptera canadensis</i> (Macquart)	PR	6.13	S	L	R	1	R	NA	NA	O
Sepsidae										
<i>Enicita annulipes</i> (Meigen)	SA	3.50	S	M	I	2	R	M	L	F
<i>Enicomira minor</i> (Haliday)	SA	3.13	G	M	I	2	R	M	L	F
<i>Meropolis stercorarius</i> (Robineau-Desvoidy)	SA	3.75	G	M	R	1	R	M	NA	F
<i>Nemopoda nitidula</i> (Fallén)	SA	4.67	G	M	I	2	C	M	L	F
<i>Saltella sphondylii</i> (Schrank)	SA	3.33	S	M	R	1	R	M	P	F
<i>Sepsis punctum</i> (Fabricius)	SA	4.17	G	M	B	4	C	M	L	F
Agromyzidae										

<i>Agromyza albipennis</i> Meigen	PH	2.93	G	L	R	1	R	M	P	F
<i>Agromyza ?bispinata</i> Spencer	PH	2.33	NA	T	R	2	R	M	P	F
<i>Agromyza facilis</i> Spencer	PH	2.13	NA	T	R	1	R	M	P	F
<i>Agromyza</i> ♀ <i>aristata/marmorensis</i>										
<i>Agromyza</i> ♀ <i>facilis/bispinata</i>										
<i>Amauromyza karli</i> (Hendel)	PH	1.87	S	T	R	1	R	M	P	F
<i>Calycomyza</i> sp.	PH	2.93	G	T	R	1	R	M	P	F
<i>Cerodontha eucaricis</i> Nowakowski	PH	2.00	S	T	R	1	R	M	A	F
<i>Cerodontha</i> (<i>Poemyza</i>) ♀ ♀ spp.										
<i>Cerodontha calamagrostidis</i> Nowakowski	PH	1.60	G	T	R	2	R	M	A	F
<i>Cerodontha dorsalis</i> (Loew)	PH	2.27	G	T	B	2	R	M	A	F
<i>Cerodontha incisa</i> (Meigen)	PH	2.37	G	T	R	1	R	M	A	F
<i>Cerodontha longipennis</i> (Loew)	PH	2.37	S	T	I	2	R	M	A	F
<i>Cerodontha magnicornis</i> Meigen	PH	2.00	S	T	B	2	R	M	A	F
<i>Hexomyza/Ophiomyia</i> sp.	PH	2.00	S	T	R	1	R	NA	P	F
<i>Liriomyza</i> sp.1	PH	1.73	S	T	R	1	R	M	P	F
<i>Liriomyza</i> sp.2	PH	1.87	S	T	R	1	R	M	P	F
<i>Metopomyza interfrontalis</i> (Melander)	PH	1.40	S	T	B	2	R	M	P	F
<i>Phytoliriomyza</i> sp.	PH	1.73	S	M	R	1	R	M	P	F
<i>Phytomyza ilicicola</i> Loew	PH	1.00	S	T	R	1	R	NA	P	F
<i>Phytomyza</i> sp.	PH	1.53	S	M	R	1	R	M	P	F
Anthomyzidae										
Anthomyzidae sp.1	PH	2.67	NA	M	R	1	R	NA	NA	A
Anthomyzidae sp.2	PH	2.47	NA	M	R	1	R	NA	NA	A
Anthomyzidae sp.3	PH	2.60	NA	M	R	1	R	NA	NA	A
Aulacigastridae										
<i>Aulacigaster leucopeza</i> (Meigen)	SA	2.93	S	T	R	1	R	U	NA	F
Clusiidae										
<i>Clusiodes johnsoni nigripalpis</i> Malloch	SA	5.00	G	M	R	1	R	NA	P	F
<i>Clusia lateralis</i> Walker	SA	3.67	NA	M	R	1	R	NA	P	F
<i>Sobarocephala atricornis</i> (Sabrosky & Steyskal)	SA	3.33	NA	M	R	2	R	U	P	F
<i>Sobarocephala flaviseta</i> (Johnson)	SA	6.00	NA	M	R	1	R	U	P	F
<i>Sobarocephala latifrons</i> (Loew)	SA	3.10	NA	M	I	3	R	U	P	F
<i>Sobarocephala setipes</i> Melander & Argo	SA	3.17	NA	M	I	2	R	U	P	F

Opomyzidae										
<i>Geomyza tripunctata</i> Fallén	PH	3.33	S	T	R	1	R	NA	NA	F
Periscelididae										
<i>Cyamops halterata</i> Sabrosky	SA	2.57	NA	M	B	3	R	U	L	A
<i>Cyamops nebulosa</i> Melander	SA	3.13	NA	M	R	2	R	U	L	A
Carnidae										
<i>Meoneura</i> sp.	SA	1.50	NA	T	I	2	R	NA	NA	NA
Chloropidae										
<i>Apallates coxendix</i> (Fitch)	SA	1.67	NA	NA	R	1	R	M	NA	O
<i>Apallates neocoxendix</i> (Sabrosky)	SA	1.70	NA	NA	I	2	R	M	NA	NA
<i>Apallates particeps</i> (Becker)	SA	1.67	NA	NA	I	2	R	M	NA	F
<i>Aphanotrigonum scabrum</i> (Aldrich)	SA	2.07	G	T	R	1	R	M	A	F
<i>Aphanotrigonum trilineatum</i> (Meigen)	SA	2.53	G	T	R	1	R	M	A	F
<i>Apotropina itascaae</i> (Sabrosky)	SA	2.07	NA	NA	I	2	R	M	NA	NA
<i>Apotropina shewelli</i> (Sabrosky)	SA	2.17	NA	NA	R	1	R	M	NA	NA
<i>Calamoncosis glyceriae</i> Nartshuk	PH	1.53	S	T	R	1	R	M	L	F
<i>Chlorops cinerapennis</i> Adams	PH	4.07	S	M	R	1	R	M	L	NA
<i>Chlorops</i> sp.1	PH	2.43	S	M	R	2	R	M	L	F
<i>Chlorops</i> sp.2	PH	2.57	S	M	R	2	R	M	L	F
<i>Chlorops</i> sp.3	PH	2.77	S	M	I	2	C	M	L	F
<i>Conioscinella</i> sp.A	PH	2.00	NA	T	R	1	R	NA	A	F
<i>Conioscinella zetttersdti</i> Andersson	PH	1.80	G	T	I	2	C	M	A	F
<i>Cryptonevra diadema</i>	PH	2.57	S	T	R	2	R	M	L	F
<i>Dasyopa</i> sp.	SA	1.33	NA	T	R	1	R	M	NA	O
<i>Dicraeus fennicus</i> Duda	PH	1.80	S	M	R	1	R	U	L	F
<i>Elachiptera angusta</i> Sabrosky	SA	2.87	G	T	R	2	R	M	A	F
<i>Elachiptera costata</i> (Loew)	SA	2.57	G	T	B	3	R	M	A	F
<i>Elachiptera erythropleura</i> Sabrosky	SA	2.60	G	T	I	2	R	M	A	F
<i>Elachiptera nigriceps</i> (Loew)	SA	2.33	G	T	B	4	C	M	A	F
<i>Elachiptera vittata</i> Sabrosky	SA	2.83	G	T	I	2	R	M	A	F
<i>Epichlorops scaber</i> (Coquillett)	PH	3.07	NA	NA	R	1	R	M	L	NA
<i>Eribolus longulus</i> (Loew)	SA	2.93	S	M	B	3	R	M	A	F
<i>Eugaurax floridensis</i> Malloch	PH	2.13	S	NA	R	1	R	M	NA	NA
<i>Gaurax apicalis</i> Malloch	SA	2.17	G	M	R	2	R	M	NA	F

<i>Gaurax dorsalis</i> (Loew)	SA	2.50	G	M	R	1	R	M	NA	F
<i>Gaurax festivus</i> Loew	SA	1.67	G	M	R	1	R	M	NA	F
<i>Gaurax ?maculicornis</i> Sabrosky	SA	2.00	G	M	R	1	R	M	NA	F
<i>Gaurax montanus</i> Coquillett	SA	2.10	G	M	R	1	R	M	NA	F
<i>Gaurax splendidus</i> Malloch	SA	2.07	G	M	R	2	R	M	NA	F
<i>Hippelates plebejus</i> Loew	SA	2.00	G	M	I	2	R	M	NA	NA
<i>Incertella bispina</i> (Malloch)	PH	1.73	S	T	B	3	C	M	L	F
<i>Incertella minor</i> (Adams)	PH	1.40	S	T	B	2	R	M	L	F
<i>Liohippelates bishoppi</i> (Sabrosky)	SA	1.93	NA	NA	B	2	C	M	NA	NA
<i>Malloewia abdominalis</i> (Becker)	SA	1.77	NA	NA	B	3	C	M	NA	NA
<i>Malloewia</i> n.sp.A TAW	SA	1.73	NA	NA	I	2	R	M	NA	NA
<i>Malloewia nigripalpis</i> (Malloch)	SA	1.73	NA	NA	R	1	R	M	NA	NA
<i>Meromyza</i> sp.	PH	3.33	G	NA	R	1	R	M	L	F
<i>Olcella</i> n.sp. near <i>parva</i> TAW	PH	1.60	NA	NA	R	1	R	M	L	NA
<i>Olcella trigramma</i> Loew	PH	1.53	NA	NA	R	2	R	M	L	NA
<i>Oscinella</i> sp.1	PH	1.67	G	T	I	2	C	M	L	F
<i>Oscinella</i> sp.2	PH	1.53	G	T	I	2	C	M	L	F
<i>Oscinella</i> sp.3	PH	1.37	G	T	R	1	R	M	L	F
<i>Oscinella</i> sp.4	PH	1.57	G	T	R	1	R	M	L	F
<i>Pseudopachychaeta approximatonervis</i> (Zetterstedt)	PH	1.87	S	M	I	2	R	U	A	A
<i>Rhopalopterum carbonarium</i> (Loew)	PH	2.03	G	NA	B	3	C	M	L	A
<i>Rhopalopterum luteiceps</i> (Sabrosky)	PH	1.47	G	NA	R	1	R	M	L	A
<i>Rhopalopterum painteri</i> (Sabrosky)	PH	1.90	G	NA	I	2	C	M	L	A
<i>Rhopalopterum soror</i> (Macquart)	PH	1.50	G	NA	I	2	R	M	L	A
<i>Rhopalopterum umbrosum</i> (Loew)	PH	1.97	G	NA	B	3	C	M	L	A
<i>Speccafrons mallochi</i> (Sabrosky)	PR	2.00	S	T	R	1	R	M	NA	F
<i>Thaumatomyia glabra</i> (Meigen)	PR	2.23	S	T	B	2	R	M	A	F
<i>Thaumatomyia grata</i> (Loew)	PR	2.60	S	T	R	2	R	M	A	F
<i>Thaumatomyia pulla</i> (Adams)	PR	1.93	S	T	R	1	R	M	A	F
<i>Thaumatomyia</i> sp.1	PR	2.37	S	T	R	1	R	M	A	F
<i>Tricimba melancholica</i> (Becker)	SA	1.83	G	M	B	3	R	M	A	F
<i>Tricimba trisulcata</i> Adams	SA	2.20	G	M	I	2	R	M	A	F

Milichiidae

<i>Neophyllomyza gaulti</i> Brochu & Wheeler	SA	1.77	S	M	R	2	R	U	NA	F
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<i>Paramyia nitens</i> (Loew)	SA	1.80	G	NA	I	2	R	NA	NA	F
Heleomyzidae										
<i>Allophyla atricornis</i> (Meigen)	SA	4.67	NA	M	R	1	R	U	A	F
<i>Suilla longipennis</i> (Loew)	SA	6.20	G	M	R	1	R	U	A	F
Sphaeroceridae										
<i>Aptilotus nigriphallus</i> Marshall & Smith	SA	2.20	NA	NA	R	1	R	NA	NA	NA
<i>Coproica acutangula</i> (Zetterstedt)	SA	1.93	G	T	I	2	R	NA	NA	F
<i>Coproica ferruginata</i> (Stenhammar)	SA	1.77	G	T	B	2	R	NA	NA	F
<i>Coproica hirtula</i> (Rondani)	SA	1.27	G	T	B	2	R	NA	NA	F
<i>Copromyza neglecta</i> (Malloch)	SA	3.23	G	T	R	2	R	M	A	F
<i>Coproica</i> sp.1	SA	1.37	G	T	R	1	R	NA	NA	F
<i>Dahlimosina dahli</i> (Duda)	SA	1.20		M	I	2	R	NA	NA	O
<i>Elachisoma</i> sp.	SA	1.07	G	T	R	1	R	NA	NA	F
<i>Ischiolepta intermedia</i> Han and Kim	SA	2.67	G	M	R	2	R	NA	NA	F
<i>Ischiolepta pusilla</i> (Fallén)	SA	2.00	G	M	I	2	R	NA	NA	F
<i>Leptocera erythrocerca</i> (Becker)	SA	2.33	G	M	B	4	C	M	P	F
<i>Limosiniinae</i> sp.1	SA	1.33	NA	NA	I	2	R	NA	NA	NA
<i>Mesosphaerocera annulicornis</i> (Malloch)	SA	3.13	NA	NA	I	2	R	NA	NA	NA
<i>Minilimosina</i> ♀♀spp.										
<i>Minilimosina</i> sp.1	SA	1.33	G	M	R	1	R	NA	NA	F
<i>Minilimosina</i> sp.2	SA	1.13	G	M	R	1	R	NA	NA	F
<i>Opalimosina mirabilis</i> (Collin)	SA	1.60	S	T	B	3	C	NA	NA	F
<i>Phthitia ovicercus</i> Marshall	SA	1.47	G	M	R	1	R	NA	NA	O
<i>Phthitia plumosula</i> (Rondani)	SA	2.00	G	M	R	1	R	NA	NA	A
<i>Phthitia quadricercus</i> Marshall	SA	1.70	G	M	I	2	R	NA	NA	A
<i>Pseudocollinella</i> sp.1	SA	2.27	S	M	R	2	C	NA	NA	O
<i>Pterogramma palliceus</i> (Johson)	SA	1.77	G	NA	I	2	C	NA	NA	F
<i>Pullimosina pullula</i> (Zetterstedt)	SA	1.93	G	M	B	3	R	NA	NA	O
<i>Pullimosina</i> sp.1	SA	1.53	G	M	R	1	R	NA	NA	O
<i>Rachispoda canadensis</i> Wheeler	SA	1.93	NA	M	R	2	R	M	P	F
<i>Rachispoda frosti</i> (Malloch)	SA	2.33	NA	M	R	1	R	M	P	F
<i>Rachispoda limosa</i> (Fallén)	SA	2.60	G	M	R	2	C	M	P	F
<i>Rachispoda</i> n.sp.1 TAW	SA	2.33	NA	M	R	1	R	M	P	F
<i>Rachispoda subpiligera</i> (Malloch)	SA	2.93	NA	M	I	2	R	M	P	F

<i>Spelobia brevipteryx</i> Marshall	SA	1.73	G	T	R	1	R	NA	NA	F
<i>Spelobia frustrilabis</i> Marshall	SA	1.90	G	M	B	2	R	NA	NA	F
<i>Spelobia luteilabris</i> (Rondani)	SA	2.03	G	T	R	2	R	NA	NA	F
<i>Spelobia maculipennis</i> (Spuler)	SA	1.73	G	M	R	2	R	M	NA	A
<i>Spelobia ochripes</i> (Meigen)	SA	2.33	G	M	B	4	C	M	A	F
<i>Spelobia pappi</i> Roháček	SA	2.13	G	M	R	2	R	NA	NA	O
<i>Spelobia semioculata</i> (Richards)	SA	1.37	G	T	R	1	R	M	NA	F
<i>Spelobia</i> sp.A	SA	1.77	G	NA	I	2	R	NA	NA	NA
<i>Spelobia</i> sp.B	SA	2.00	G	NA	R	2	R	NA	NA	NA
<i>Spelobia</i> sp.C	SA	1.87	G	NA	B	2	R	NA	NA	NA
<i>Terrilimosina</i> sp.1	SA	1.40	G	M	I	2	R	NA	NA	F
<i>Trachypella nuda</i> Roháček & Marshall	SA	1.60	G	T	B	2	R	NA	NA	A
Diastatidae										
<i>Diastata pulchra</i> Loew	NA	0.00	NA	M	R	1	R	NA	NA	NA
<i>Diastata</i> sp.1	NA	0.00	NA	M	R	1	R	NA	NA	NA
<i>Diastata</i> sp.2	NA	0.00	NA	M	R	1	R	NA	NA	NA
Drosophilidae										
<i>Chymomyza amoena</i> (Loew)	SA	2.60	G	NA	I	2	C	NA	NA	NA
<i>Drosophila</i> (<i>Melanica</i> group) sp.1	NA	2.40	NA	NA	I	2	R	NA	A	
<i>Drosophila macrospina</i> Stalker & Spencer	NA	2.40	NA	NA	I	2	C	NA	A	NA
<i>Drosophila nr. transversa</i> sp.	NA	2.50	NA	NA	I	2	R	NA	A	NA
<i>Drosophila putrida</i> Sturtevant	NA	2.53	NA	NA	I	2	R	NA	A	NA
<i>Drosophila quinaria</i> Loew	NA	2.20	NA	NA	R	1	R	NA	A	NA
<i>Drosophila</i> sp.7	NA	1.90	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.9	NA	1.47	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.10	NA	2.67	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.11	NA	3.17	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.12	NA	2.67	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.13	NA	2.67	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.14	NA	2.27	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.15	NA	2.27	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila</i> sp.16	NA	2.60	NA	NA	NA	NA	R	NA	A	NA
<i>Drosophila testacea</i> Roser	NA	2.33	NA	NA	I	2	C	NA	A	NA
<i>Drosophila transversa</i> Fallén	NA	2.50	NA	NA	I	3	C	NA	A	NA

<i>Drosophila tripunctata</i> Loew	PH	2.27	NA	NA	R	2	R	NA	A	NA
<i>Scaptomyza (Hemiscaptomyza) ?trochanterata</i> Collin	PH	2.30	NA	T	I	2	R	M	P	F
<i>Scaptomyza (Scaptomyza) flaveola</i> Meigen	PH	1.83	G	T	R	2	R	M	P	F
<i>Scaptomyza adusta</i> (Loew)	PH	2.33	G	T	I	2	R	M	P	NA
<i>Scaptomyza pallida</i> (Zetterstedt)	PH	2.17	S	T	B	3	C	M	P	F
Ephydriidae										
<i>Allotrichoma simplex</i> (Loew)	SA	1.83	G	M	I	2	R	NA	NA	O
<i>Allotrichoma</i> ♀♀ spp.										
<i>Athyroglossa granulosa</i> (Cresson)	SA	2.17	G	L	I	2	C	NA	NA	A
<i>Axysta nigrifacies</i> Miyagi	SA	1.40	S	L	R	1	R	NA	NA	NA
<i>Brachydeutera argentata</i> (Walker)	SA	3.37	G	L	I	2	R	NA	NA	O
<i>Coenia curvicauda</i> (Meigen)	SA	2.93	G	L	I	2	C	NA	NA	O
<i>Discocerina obscurella</i> (Fallén)	SA	2.20	G	L	I	2	R	M	NA	O
<i>Ditrichophora atrata</i> Cresson	SA	2.13	NA	L	I	2	C	NA	NA	NA
<i>Ditrichophara exigua</i> Cresson	SA	1.70	NA	L	B	3	C	NA	NA	NA
<i>Ditrichophora valens</i> Cresson	SA	2.40	NA	L	R	1	R	NA	NA	NA
<i>Hyadina albovenosa</i> Coquillett	SA	1.37	S	L	R	2	R	NA	NA	F
<i>Hyadina vockerothi</i> Clausen	SA	1.27	S	L	R	1	R	NA	NA	F
<i>Hydrellia ?trichaeta</i> Cresson	PH	2.27	G	L	R	1	R	NA	L	F
<i>Hydrellia americana</i> Cresson	PH	1.40	G	L	B	3	R	NA	L	F
<i>Hydrellia griseola</i> (Fallén)	PH	2.27	G	L	I	3	R	NA	L	F
<i>Hydrellia</i> sp.1	PH	2.73	G	L	R	1	R	NA	L	F
<i>Hydrellia</i> sp.2	PH	1.97	G	L	I	2	R	NA	L	F
<i>Ilythea spilota</i> (Curtis)	SA	2.20	S	L	R	2	R	NA	NA	F
<i>Nostima picta</i> (Fallén)	SA	1.30	S	L	I	2	R	NA	NA	F
<i>Notiphila (Dichaeta) caudata</i> group										
<i>Notiphila (Dichaeta) decoris</i> Williston	SA	4.07	S	L	R	1	R	M	L	O
<i>Notiphila (Dichaeta) olivacea</i> Cresson	SA	5.00	S	L	B	3	C	M	L	O
<i>Notiphila (Dichaeta) scalaris</i> Loew	SA	4.13	S	L	I	2	R	M	L	O
<i>Notiphila (Dichaeta)</i> sp.	SA	4.13	S	L	I	2	R	M	L	O
<i>Notiphila (Notiphila) avia</i> Loew	SA	4.83	S	L	I	2	C	M	L	O
<i>Notiphila (Notiphila) nudipes</i> Cresson	SA	4.13	S	L	I	2	R	M	L	O
<i>Notiphila (Notiphila) paouroura</i> Mathis	SA	3.67	S	L	I	2	R	M	L	O
<i>Notiphila (Notiphila) phaeopsis</i> Mathis	SA	3.40	S	L	I	2	R	M	L	O

<i>Notiphila (Notiphila) solita</i> Walker	SA	3.50	S	L	I	2	R	M	L	O
<i>Notiphila</i> ♀♀? <i>pauroura</i> Mathis										
<i>Ochtera borealis</i> Clausen	PR	5.57	S	L	R	1	R	NA	NA	F
<i>Paracoenia (Paracoenia) fumosalis</i> Cresson	SA	3.67	NA	L	R	1	R	NA	NA	O
<i>Parydra (Parydra) quadrituberculata</i> Loew	PH	3.40	NA	M	I	2	R	NA	A	F
<i>Parydra (Parydra)</i> ♀♀ spp.										
<i>Philotelma alaskensis</i> Cresson	SA	1.37	NA	L	R	2	R	NA	NA	NA
<i>Philygria debilis</i> Loew	PH	1.40	NA	L	I	2	R	NA	NA	F
<i>Platygympnopa helicis</i> Wirth	SA	2.57	G	M	R	1	R	NA	NA	A
<i>Polytrichophora orbitalis</i> (Loew)	SA	1.97	NA	L	I	2	R	NA	NA	F
<i>Psilopa olga</i> Cresson	PH	1.40	NA	T	R	1	R	NA	NA	F
<i>Scatella (Scatella) stagnalis</i> Fallén	SA	2.00	G	L	B	4	C	NA	NA	F
Calliphoridae										
<i>Lucilia coeruleiviridis</i> (Macquart)	SA	7.08	G	T	R	2	R	M	L	F
<i>Lucilia illustris</i> (Meigen)	SA	8.13	G	T	B	2	R	M	L	F
<i>Lucilia silvarium</i> Meigen	SA	6.88	G	T	I	2	R	M	L	F
<i>Pollenia griseotomentosa</i> (Jacentkovsky)	PA	6.04	S	M	I	2	R	M	A	F
<i>Pollenia labialis</i> Robineau-Desvoidy	PA	8.63	S	M	R	2	R	M	A	F
<i>Pollenia pediculata</i> Macquart	PA	8.21	S	M	B	3	R	M	A	F
<i>Pollenia rudis</i> (Fabricius)	PA	8.33	S	M	R	1	R	M	A	F
Sarcophagidae										
<i>Blaesoxipha (Acridiophaga) hunteri</i> (Hough)	PA	6.25	S	T	R	2	R	M	P	F
<i>Blaesoxipha (Acridiophaga) kyrtonidion</i> Pape	PA	6.67	S	T	R	1	R	M	P	F
<i>Blaesoxipha (Servaisia) uncata</i> (Wulp)	PA	8.33	S	T	R	1	R	M	P	F
<i>Boettcheria bisetosa</i> Parker	SA	10.42	G	T	I	2	R	M	P	F
<i>Boettcheria cimbicis</i> (Townsend)	PA	7.92	G	T	I	2	C	U	P	F
<i>Boettcheria latisterna</i> Parker	PA	8.75	G	T	R	2	R	U	P	F
<i>Brachicoma devia</i> (Fallén)	PA	7.50	G	T	R	1	R	M	P	F
<i>Brachicoma sarcophagina</i> (Townsend)	PA	6.96	G	T	R	2	R	M	P	F
<i>Helicobia</i> ♀♀ spp.										
<i>Helicobia rapax</i> (Walker)	SA	4.54	G	T	R	2	R	M	P	F
<i>Helicobia stellata</i> (Wulp)	SA	3.75	G	T	R	1	R	M	P	F
<i>Oxysarcodexia cingarus</i> (Aldrich)	SA	7.92	NA	T	R	1	R	M	P	F
<i>Ravinia querula</i> (Walker)	SA	10.21	NA	T	R	2	R	M	P	F

<i>Ravinia stimulans</i> (Walker)	SA	7.08	NA	T	B	2	R	M	P	F
<i>Sarcophaga (Robineauella) nearctica</i> Parker	SA	10.42		T	I	2	R	M	P	F
<i>Sarcophaga</i> sp.1	NA	9.38	NA	T	B	2	R	M	P	F
<i>Sarcophaga subvicina</i> Rohdendorf	PA	10.00		T	I	2	R	M	P	F
<i>Sarcophaginae</i> sp.1	NA	7.50	NA	T	I	2	R	M	P	F
<i>Sarcotachinella sinuata</i> (Meigen)	PA	6.67		T	I	3	C	M	P	F
Scathophagidae										
<i>Chaetosa (Chaetosa) punctipes</i> Meigen	PH	4.50	NA	M	R	1	R	M	NA	A
<i>Scathophaga stercoraria</i> (Linnaeus)	SA	7.33	G	T	R	1	R	M	NA	F

Appendix 2.2. Coordinates, surrounding landscape, local and chemical variables and ground cover attributes at each of the 12 wetland sites. Water table level was determined following these categories: 1. Water level below surface, 2. Water level at surface, 3. Water level less than 1 m above surface, 4. Water level more than 1 m above surface.

		Swamp				Marsh				Bog			
		CAL_SW	TIH_SW	OKA_SW	LAZ_SW	BER_MA	OKA_MA	MIL_MA	FOR_MA	BLA_BG	PIN_BG	MIR_BG	BRB_BG
Coordinates	Decimal latitude	45.505	45.274	45.470	45.417	45.385	45.487	45.661	45.559	45.703	45.096	45.685	45.125
	Decimal longitude	-73.963	-73.952	-74.058	-74.180	-73.755	-74.007	-73.928	-74.385	-73.830	-73.865	-74.039	-74.223
Surrounding landscape	Open Water (%)	44.09	42.11	26.39	0.22	27.22	21.12	0.10	35.68	0.19	1.37	0.49	0.00
	Exposed land (%)	1.64	3.48	4.32	3.37	1.34	1.17	2.02	0.82	4.97	9.05	9.39	4.51
	Urban development (%)	28.56	2.61	3.85	23.80	28.44	7.99	6.34	2.53	17.53	1.37	18.27	0.45
	Low vegetation (%)	4.33	1.77	3.43	4.50	5.79	10.62	11.44	4.60	8.16	6.03	9.42	4.42
	Wetlands (%)	0.20	3.65	3.71	0.79	15.33	6.66	0.24	0.03	9.30	20.49	5.41	39.08
	Agriculture (%)	10.33	43.62	20.59	7.19	7.36	20.86	31.92	28.92	9.24	22.37	34.29	25.09
	Forest (%)	10.85	2.76	37.72	60.13	14.52	31.38	47.94	27.42	50.61	39.31	22.74	26.45
	Area (ha)	143.2	13.8	50.9	60.6	43.3	86.7	19.9	6.7	65.3	16.6	67.5	161.6
Local and chemical	Tree cover (%)	85	80	90	95	2	50	1	0	1	20	1	25
	Water above surface (%)	25	60	40	50	30	60	30	90	0	10	0	0
	Water table level	3	3	3	3	4	3	3	4	2	2	1	1
	Fluctuation (cm)	15	24	21.8	51	6	14.5	6.5	3	4	0	0	0
	pH	6.8	7.8	7.1	7.7	7.2	7.3	5.8	7.8	4.4	5.1	4.7	3.7
	Temperature (°C)	20.1	19.4	21.1	17.3	23.0	23.4	24.0	20.7	23.8	23.1	24.9	19.7
	Conductivity (µS/m)	612	556	467	732	203	392	49	457	28	94	31	81
Ground cover	<i>Abies balsamea</i>	0	0	0	10	0	0	0	0	0	0	0	0
	<i>Acer saccharinum</i>	0	0	0	0	0	4	0	0	0	0	0	0
	<i>Alnus incana</i>	0	0	0	0	0	0	0	0	4	0	0	0
	<i>Amphicarpa bracteata</i>	0	3	0	0	0	0	0	0	0	0	0	0
	bare soil	38	0	0	0	0	7	0	6	0	0	0	0

<i>Betula alleghaniensis</i>	0	0	0	10	0	0	0	0	0	0	0	0
<i>Betula populifolia</i>	0	0	0	0	0	0	6	0	0	4	0	6
<i>Boehmeria cylindrica</i>	0	0	0	0	0	0	0	8	0	0	0	0
? <i>Calla palustris</i>	0	0	0	12	0	0	0	0	0	0	0	0
<i>Carex crinita</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Carex oligosperma</i>	0	0	0	0	0	0	0	0	69	52	0	0
<i>Carex pseudo-cyperus</i>	0	0	0	0	2	0	0	0	0	0	0	0
<i>Carex viridula</i>	0	0	0	18	0	0	0	0	0	0	0	0
<i>Cephalanthus occidentalis</i>	0	0	17	0	0	16	0	0	0	0	0	0
<i>Chamaedaphne calyculata</i>	0	0	0	0	0	0	0	0	47	25	4	0
<i>Cicuta maculata</i>	0	0	0	2	0	0	0	0	0	0	0	0
<i>Cladonia spp.</i>	0	0	0	0	0	0	0	0	0	0	0	3
<i>Cornus stolonifera</i>	0	25	0	0	0	0	0	0	0	0	0	0
dead wood	0	15	23	2	0	9	0	0	0	0	0	0
<i>Drosera rotundifolia</i>	0	0	0	0	0	0	0	0	21	0	0	0
<i>Equisetum fluviatile</i>	0	0	3	0	0	0	0	0	0	0	0	0
<i>Equisetum pratense</i>	16	4	0	16	0	0	0	0	0	0	0	0
<i>Eriophorum vaginatum</i>	0	0	0	0	0	0	0	0	3	0	9	2.4
<i>Fraxinus nigra</i>	17	0	0	0	0	0	0	0	0	0	0	0
<i>Glyceria canadensis</i>	0	0	0	0	0	0	1	0	0	0	0	0
herb sp. (? <i>Galium</i>)	0	0	0	2	0	0	0	7	0	0	0	0
<i>Hydrocharis morsus-ranae</i>	0	3	4	0	48	7	0	42	0	0	0	0

<i>Kalmia angustifolia</i>	0	0	0	0	0	0	0	0	0	0	60	29
<i>Larix laricina</i>	0	0	0	0	0	0	16	0	0	0	6	0
<i>Ledum groenlandicum</i>	0	0	0	0	0	0	0	0	0	0	11	0
litter	50	53	83	42	24	73	0	33	0	13	21	55
<i>Lysimachia terrestris</i>	0	0	0	0	0	0	0	0	0	12.4	0	0
<i>Maianthemum canadense</i>	0	0	0	1	0	0	0	0	0	0	0	0
<i>Onoclea sensibilis</i>	60	0	13	23	0	27	0	0	0	0	0	0
Open pool	0	51	10	34	59	21	0	50	0	0	0	0
<i>Osmunda cinnamomea</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Osmunda regalis</i>	36	0	4	0	0	0	0	0	0	0	0	0
<i>Phalaris arundinacea</i>	0	0	0	0	39	0	0	0	0	0	0	0
<i>Phragmites australis</i>	0	12	0	0	0	0	0	0	0	0	0	0
<i>Pinus rigida</i>	0	0	0	0	0	0	0	0	0	10	0	0
<i>Pleurocarpus moss</i>	16	15	11.8	20	8	3.4	0	1	0	0	0	0
<i>Polytrichum spp.</i>	0	0	0	0	0	0	0	0	17	10	66	47
<i>Potentilla palustris</i>	0	0	0	0	0	4	0	0	0	0	0	0
<i>Sagittaria latifolia</i>	0	0	0	0	53	24	0	0	0	0	0	0
<i>Sagittaria rigida</i>	0	0	0	0	7	0	0	0	0	0	0	0
<i>Salix candida</i>	0	0	0	0	0	0	0	0	0	2	0	0
<i>Salix pedicellaris</i>	0	0	0	0	0	0	0	0	0	0	0	21
<i>Salix pyrifolia</i>	0	0	0	0	0	0	0	0	0	17	0	0
<i>Solanum dulcamara</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Sparganium eurycarpum</i>	0	0	0	0	8	0	0	0	0	0	0	0

<i>Sphagnum spp.</i>	0	0	0	0	0	0	0	0	0	67	100	91	20
<i>Spiraea alba</i>	0	0	0	0	0	0	0	0	0	0	12	0	0
<i>Spirodela polyrhiza</i>	0	0	0	0	26	0	0	49	0	0	0	0	0
<i>Thuja occidentalis</i>	0	0	0	8	0	0	0	0	0	0	0	0	0
<i>Toxicodendron radicans</i>	17	0	0	5	0	0	0	0	0	0	0	0	0
<i>Trientalis borealis</i>	0	0	0	4	0	0	0	0	0	0	0	0	0
<i>Typha angustifolia</i>	0	0	0	0	20	0	0	21	0	0	0	0	0
<i>Vaccinium ?angustifolium</i>	0	0	0	0	0	0	0	0	0	0	0	28	0
<i>Vaccinium myrtilloides</i>	0	0	0	0	0	0	0	0	0	0	0	0	53
<i>Vitis riparia</i>	0	5	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.3. Abundance of Schizophora species and morphospecies collected from each of the 12 wetland sites. Species in grey were excluded from analyses.

Species	Code	Swamp				Marsh				Bog			
		CAL_SW	TIH_SW	OKA_SW	LAZ_SW	BER_MA	OKA_MA	MIL_MA	FOR_MA	BLA_BG	PIN_BG	MIR_BG	BRB_BG
Micropezidae													
<i>Compsobata (Compsobata) sp.</i>	comp_sp	0	1	0	0	0	0	0	0	0	0	0	0
<i>Rainieria antennaepes</i> (Say)	raini_ant	0	3	0	0	0	0	0	0	0	0	0	0
Lonchaeidae													
<i>Lonchaea sp.</i>	lonch_sp	0	0	1	0	0	1	0	0	0	0	0	0
Pallopteridae													
<i>Temnosira subarcuata</i> Johnson	temn_sub	1	0	0	0	0	0	0	0	0	0	0	0
Platystomatidae													
<i>Riviella pallida</i> Loew	rivi_pall	1	0	4	0	0	0	0	0	0	0	0	0
<i>Riviella sp.1</i>	rivi_sp1	1	4	0	0	0	0	0	0	0	0	0	0
<i>Riviella sp.2</i>	rivi_sp2	0	9	0	0	0	1	0	0	0	0	0	0
<i>Riviella steyskali</i> Namba	rivi_ste	0	0	0	0	0	0	0	0	0	0	0	1
<i>Riviella variabilis</i> Loew	rivi_var	1	0	0	0	0	7	0	0	0	0	0	0
Tephritidae													
<i>Euaresta bella</i> (Loew)	euar_bell	0	0	1	0	0	0	3	0	1	4	10	21
<i>Euleia fratria</i> (Loew)	eule_fra	0	1	0	0	0	0	0	0	0	0	0	0
<i>Ictericia seriata</i> (Loew)	icte_ser	0	0	0	0	0	1	0	0	0	0	0	0
<i>Paroxyna albiceps</i> (Loew)	parox_alb	0	0	0	0	0	0	0	0	0	0	0	1
<i>Rhagoletis pomonella</i> (Walsh)	rha_pom	0	0	0	0	0	0	0	0	0	0	0	1
<i>Urophora quadrifasciata</i> (Meigen)	urop_qua	0	0	0	0	0	0	1	0	0	0	0	0
Ulidiidae													
<i>Chaetopsis fulfivrons</i> (Macquart)	chae_fulv	0	0	0	0	0	0	3	3	0	0	0	0
<i>Chaetopsis massyla</i> (Walker)	chae_mass	0	0	0	0	6	0	2	4	0	0	2	0
<i>Euxesta notata</i> Wiedemann	euxe_not	0	1	0	0	0	1	1	0	0	0	0	0
<i>Meliera similis</i> (Loew)	meli_sim	0	0	0	0	0	0	3	0	0	0	0	0
Chamaemyiidae													
<i>Leucopis americana</i> Malloch	leuc_ame	0	0	0	0	0	0	0	0	0	0	0	1
<i>Leucopis sp.</i>	leuc_sp	0	0	0	0	0	0	1	0	0	0	0	0
Lauxaniidae													
<i>Camptoprosopa sp.</i>	campt_sp	0	0	0	0	0	0	1	0	0	0	0	0
<i>Homoneura (Homoneura) incerta</i> (Malloch)	homo_inc	0	0	2	0	0	0	0	0	0	0	0	0
<i>Homoneura (Homoneura) pernotata</i> (Malloch)	homo_pern	4	0	0	1	0	0	0	0	0	0	0	1
<i>Homoneura (Homoneura) philadelphica</i> (Macquart)	homo_phi	16	0	0	0	0	0	0	0	0	0	0	2

<i>Homoneura (Homoneura) ♀♀aequalis</i> group		0	1	0	0	0	0	0	0	0	0	0	0
<i>Homoneura (Tarsohomoneura) americana</i> (Wiedemann)	homo_ame	0	0	0	0	0	0	0	0	0	0	0	1
<i>Homoneura (Tarsohomoneura) houghii</i> (Coquillett)	homo_houg	0	0	0	0	0	0	0	0	0	0	1	2
<i>Homoneura (Tarsohomoneura) sheldoni</i> (Coquillett)	homo_shel	0	0	0	0	0	0	3	0	5	1	56	3
<i>Lauxania shewelli</i> Perusse & Wheeler	laux_she	0	0	0	0	0	0	0	0	0	0	0	1
<i>Minettia (Minettia) cana</i> Melander	mine_cana	0	0	0	0	0	0	0	0	0	0	0	3
<i>Minettia (Minettia) lupulina</i> Fabricius	mine_lup	0	0	0	0	0	0	0	0	0	0	2	21
<i>Minettia lyraformis</i> Shewell	mine_lyra	0	0	0	0	0	0	0	0	0	0	0	1
<i>Poecilolycia aspinosa</i> Shewell	poe_asp	0	0	0	0	0	0	0	0	0	0	0	1
<i>Poecilolycia browni</i> Curran	poe_brow	3	0	0	2	0	0	0	0	0	0	0	1
Dryomyzidae													
<i>Dryomyza anili</i> s Fallén	dryo_ani	12	2	0	14	0	0	0	0	0	0	0	1
Sciomyzidae													
<i>Dictya ♀♀spp.</i>		0	0	0	0	1	0	1	0	0	0	1	0
<i>Dictya expansa</i> Steyskal	dict_expa	0	0	0	2	0	24	0	0	0	0	0	0
<i>Ditya pictipes</i> (Loew)	dict_pic	1	0	0	0	0	0	0	0	0	0	0	0
<i>Elgiva sollicita</i> (Harris)	elgi_soli	0	0	0	0	0	0	0	0	0	0	1	0
<i>Limnia boscii</i> (Robineau-Desvoidy)	limni_bos	0	0	0	1	0	0	4	0	0	0	0	1
<i>Limnia conica</i> Steyskal	limni_con	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pherbecta limenitis</i> Steyskal	pher_anu	0	0	0	0	0	0	0	0	7	0	0	0
<i>Pherbellia anubis</i> Knutson	pher_gris	0	0	26	1	11	57	0	0	0	0	0	0
<i>Pherbellia griseola</i> (Fallén)	pher_nan	0	0	4	0	0	0	0	0	0	0	0	0
<i>Pherbellia nana nana</i> (Fallén)	pher_qua	0	1	0	0	0	0	0	0	0	0	0	0
<i>Pherbellia quadrata</i> Steyskal	pher_vita	0	2	0	0	0	0	0	0	0	0	0	0
<i>Pherbellia vitalis</i> (Cresson)	pherb_lim	0	0	1	0	0	3	0	0	0	0	0	0
<i>Poecilographa decora</i> (Loew)	poec_dec	10	0	0	0	0	0	0	0	0	0	0	0
<i>Pteromicra pectorosa</i> (Hendel)	pter_pec	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pteromicra similis</i> Steyskal	pter_sim	0	0	8	0	5	2	0	0	0	0	0	0
<i>Sciomyza varia</i> (Coquillett)	scio_var	0	1	2	0	0	0	0	0	0	0	0	0
<i>Sepedon fuscipennis nobilis</i> Orth	sepe_fus	0	0	1	0	4	7	0	0	0	0	0	0
<i>Sepedon gracilicornis</i> Orth	sepe_grac	0	1	0	0	1	1	0	0	0	0	0	0
<i>Sepedon tenuicornis</i> Cresson	sepe_ten	0	0	6	0	0	0	0	0	0	0	0	0
<i>Tetanocera annae</i> Steyskal	teta_ann	0	0	5	0	0	1	0	0	0	0	0	0
<i>Tetanocera fuscinervis</i> Zetterstedt	teta_fus	0	0	0	0	0	0	3	0	0	0	0	0
<i>Tetanocera plebeja</i> Loew	teta_ple	0	1	1	2	0	0	2	0	0	0	0	0
<i>Tetanocera plumosa</i> Loew	teta_plu	1	0	0	0	0	0	0	0	0	0	0	1
<i>Tetanocera rotundicornis</i> Loew	teta_rot	0	0	0	0	0	1	0	0	0	0	0	0
<i>Tetanocera</i> sp.	teta_sp	1	0	0	0	0	0	0	0	0	0	0	0
<i>Tetanocera valida</i> Loew	teta_val	0	0	0	2	0	0	0	0	0	0	0	1
<i>Trypetoptera canadensis</i> (Macquart)	try_cana	0	0	0	2	0	0	0	0	0	0	0	0
Sepsidae													

<i>Enicita annulipes</i> (Meigen)	enic_ann	0	1	0	0	0	0	6	0	0	0	0	0
<i>Enicomira minor</i> (Haliday)	enic_min	0	18	0	0	1	0	0	0	0	0	0	0
<i>Meropolis stercorarius</i> (Robineau-Desvoidy)	mero_ste	0	1	0	0	0	0	0	0	0	0	0	0
<i>Nemopoda nitidula</i> (Fallén)	nemo_nit	58	0	0	0	2	0	27	0	0	0	0	0
<i>Saltella sphondylii</i> (Schrank)	salt_sph	0	0	0	0	0	0	0	0	0	0	1	0
<i>Sepsis punctum</i> (Fabricius)	seps_pun	11	5	1	4	1	6	30	0	4	3	5	8
Agromyzidae													
<i>Agromyza albipennis</i> Meigen	agro_alb	0	0	0	0	4	0	0	0	0	0	0	0
<i>Agromyza ?bispinata</i> Spencer	agro_bis	2	1	0	0	0	0	0	0	0	0	0	0
<i>Agromyza facilis</i> Spencer	agro_fac	0	0	1	0	0	0	0	0	0	0	0	0
<i>Agromyza</i> ♀ <i>aristata/marmorensis</i>		0	0	1	0	0	0	0	0	0	0	0	0
<i>Agromyza</i> ♀ <i>facilis/bispinata</i>		1	0	0	0	0	0	0	0	0	0	1	0
<i>Amauromyza karli</i> (Hendel)	amau_kar	0	0	0	0	0	0	0	0	0	1	0	0
<i>Calycomyza</i> sp.	caly_sp	0	1	0	0	0	0	0	0	0	0	0	0
<i>Cerodontha eucaricis</i> Nowakowski	cero_eul	0	0	4	0	0	0	0	0	0	0	0	0
<i>Cerodontha</i> (<i>Poemyza</i>) ♀ ♀ spp.		0	0	0	0	0	1	2	0	0	0	0	0
<i>Cerodontha calamagrostidis</i> Nowakowski	cero_cal	0	1	0	1	0	0	0	0	0	0	0	0
<i>Cerodontha dorsalis</i> (Loew)	cero_dor	0	1	0	3	2	0	0	0	1	1	0	0
<i>Cerodontha incisa</i> (Meigen)	cero_inc	0	0	0	0	3	0	0	0	0	0	0	0
<i>Cerodontha longipennis</i> (Loew)	cero_lon	0	5	2	0	0	15	0	1	0	0	0	0
<i>Cerodontha magnicornis</i> Meigen	cero_mag	0	1	5	0	0	1	0	0	0	0	1	0
<i>Hexomyza/Ophiomyia</i> sp.	hexo_sp	0	0	0	0	0	3	0	0	0	0	0	0
<i>Liriomyza</i> sp.1	liri_sp1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Liriomyza</i> sp.2	liri_sp2	0	0	0	0	1	0	0	0	0	0	0	0
<i>Melanagromyza</i> sp.	mela_sp	0	0	0	0	0	0	0	0	0	0	0	0
<i>Metopomyza interfrontalis</i> (Melander)	meto_int	0	0	0	6	1	0	9	0	0	8	1	0
<i>Phytoliriomyza</i> sp.	phytom_sp	0	0	1	0	0	0	0	0	0	0	0	0
<i>Phytomyza ilicicola</i> Loew	phyt_ili	0	0	27	0	0	0	0	0	0	0	0	0
<i>Phytomyza</i> sp.	phyt_sp	0	1	0	0	0	0	0	0	0	0	0	0
Anthomyzidae													
Anthomyzidae sp.1	antho_sp1	0	0	0	0	0	0	0	0	0	1	0	0
Anthomyzidae sp.2	antho_sp2	0	0	1	0	0	0	0	0	0	0	0	0
Anthomyzidae sp.3	antho_sp3	1	0	0	0	0	0	0	0	0	0	0	0
Aulacigastridae													
<i>Aulacigaster leucopeza</i> (Meigen)	aula_leu	0	0	1	0	0	0	0	0	0	0	0	0
Clusiidae													
<i>Clusiodes johnsoni nigripalpis</i> Malloch	clus_john	1	0	0	0	0	0	0	0	0	0	0	0
<i>Clusia lateralis</i> Walker	clus_lat	1	0	0	0	0	0	0	0	0	0	0	0
<i>Sobarocephala atricornis</i> (Sabrosky & Steyskal)	soba_atr	4	4	0	2	0	0	0	0	0	0	0	0
<i>Sobarocephala flaviseta</i> (Johnson)	soba_fla	0	1	0	0	0	0	0	0	0	0	0	0
<i>Sobarocephala latifrons</i> (Loew)	soba_lat	17	2	0	1	0	0	1	0	0	0	0	0

<i>Sobarocephala setipes</i> Melander & Argo	soba_set	8	1	3	0	0	0	2	0	0	0	0	0
Opomyzidae													
<i>Geomyza tripunctata</i> Fallén	geom_tri	0	0	0	0	0	0	1	0	0	0	0	0
Periscelididae													
<i>Cyamops halterata</i> Sabrosky	cyam_halt	0	0	1	0	1	0	1	0	10	8	1	0
<i>Cyamops nebulosa</i> Melander	cyam_neb	14	0	16	0	0	0	0	0	0	0	0	0
Carnidae													
<i>Meoneura</i> sp.	meon_sp	0	1	0	0	0	0	0	0	1	0	0	0
Chloropidae													
<i>Apallates coxendix</i> (Fitch)	app_cox	0	0	0	0	0	0	0	0	0	0	0	1
<i>Apallates neocoxendix</i> (Sabrosky)	app_neo	0	4	0	0	0	0	0	0	0	0	1	1
<i>Apallates particeps</i> (Becker)	app_par	1	0	0	0	0	0	0	0	0	0	1	0
<i>Aphanotrigonum scabrum</i> (Aldrich)	apha_sca	0	0	0	0	0	0	16	0	0	0	0	0
<i>Aphanotrigonum trilineatum</i> (Meigen)	apha_tri	0	0	0	0	0	0	4	0	0	0	0	0
<i>Apotropina itasca</i> (Sabrosky)	apot_ita	0	2	1	0	0	0	0	2	0	0	0	0
<i>Apotropina shewelli</i> (Sabrosky)	apot_she	0	3	0	0	0	0	0	0	0	0	0	0
<i>Calamoncosis glyceriae</i> Nartshuk	cala_gly	0	0	0	0	0	0	6	0	0	0	0	0
<i>Chlorops cinerapennis</i> Adams	chlo_cine	0	0	0	0	0	0	3	0	0	0	0	0
<i>Chlorops</i> sp.1	chlo_sp1	0	1	0	6	0	0	0	0	0	0	0	0
<i>Chlorops</i> sp.2	chlo_sp2	0	1	1	0	0	0	0	0	0	0	0	0
<i>Chlorops</i> sp.3	chlo_sp3	0	0	0	0	0	0	2	0	57	76	11	0
<i>Conioscinella</i> sp.A	coni_spA	0	0	0	0	0	0	2	0	0	0	0	0
<i>Conioscinella zetttersdti</i> Andersson	coni_zet	0	0	1	0	0	0	110	0	0	0	0	0
<i>Cryptonevra diadema</i>	cryp_dia	0	0	0	0	3	0	1	0	0	0	0	0
<i>Dasyopa</i> sp.	dasy_sp	0	0	0	0	0	0	0	0	0	0	0	2
<i>Dicraeus fennicus</i> Duda	dicr_fen	0	0	0	0	0	0	0	0	0	0	1	0
<i>Elachiptera angusta</i> Sabrosky	elac_ang	0	4	9	7	0	0	0	0	0	0	0	0
<i>Elachiptera costata</i> (Loew)	elac_cos	8	4	2	1	2	6	0	0	0	2	0	2
<i>Elachiptera erythropleura</i> Sabrosky	elac_ery	3	1	17	0	1	2	0	0	0	0	0	0
<i>Elachiptera nigriceps</i> (Loew)	elac_nigr	7	56	7	6	14	131	19	4	1	0	3	0
<i>Elachiptera vittata</i> Sabrosky	elac_vitt	0	0	0	1	0	0	1	0	0	0	0	0
<i>Epichlorops scaber</i> (Coquillett)	epic_sca	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eribolus longulus</i> (Loew)	erib_lon	0	1	0	0	4	1	2	20	0	0	4	0
<i>Eugaurax floridensis</i> Malloch	euga_flo	0	0	0	0	1	0	0	0	0	0	0	0
<i>Gaurax apicalis</i> Malloch	gaur_api	1	1	1	0	0	0	0	0	0	0	0	0
<i>Gaurax dorsalis</i> (Loew)	gaur_dor	2	0	0	0	0	0	0	0	0	0	0	0
<i>Gaurax festivus</i> Loew	gaur_fes	0	0	1	0	0	0	0	0	0	0	0	0
<i>Gaurax ?maculicornis</i> Sabrosky	gaur_mac	1	0	0	0	0	0	0	0	0	0	0	0
<i>Gaurax montanus</i> Coquillett	gaur_mon	2	0	0	0	0	0	0	0	0	0	0	0
<i>Gaurax splendidus</i> Malloch	gaur_spl	1	1	0	0	0	0	0	0	0	0	0	0
<i>Hippelates plebejus</i> Loew	hipp_ple	0	0	0	0	0	0	1	0	1	0	1	0

<i>Incertella bispina</i> (Malloch)	ince_bis	2	0	1	0	0	1	139	0	59	15	36	0
<i>Incertella minor</i> (Adams)	ince_min	0	0	0	1	0	0	7	0	13	2	2	0
<i>Liohippelates bishoppi</i> (Sabrosky)	lioh_bis	0	172	12	0	0	5	0	0	0	1	0	6
<i>Malloewia abdominalis</i> (Becker)	mall_abd	0	0	0	1	1	1	0	0	1	9	2	110
<i>Malloewia n.sp.A TAW</i>	mall_nsp	0	0	0	7	0	0	0	0	0	0	0	0
<i>Malloewia nigripalpis</i> (Malloch)	mall_nig	0	2	0	0	0	0	0	0	6	6	1	4
<i>Meromyza sp.</i>	mero_sp	0	0	0	0	0	0	0	0	0	0	1	0
<i>Olcella n.sp. near parva TAW</i>	olc_npar	0	0	0	0	0	0	1	0	0	0	0	0
<i>Olcella trigramma</i> Loew	olc_tri	0	0	0	0	0	0	0	0	0	0	2	7
<i>Oscinella sp.1</i>	osci_sp1	0	0	0	0	0	0	46	0	0	0	1	23
<i>Oscinella sp.2</i>	osci_sp2	0	0	0	0	64	0	8	0	0	0	0	1
<i>Oscinella sp.3</i>	osci_sp3	0	2	0	0	0	0	0	0	0	0	0	0
<i>Oscinella sp.4</i>	osci_sp4	0	0	0	2	0	0	0	0	0	0	0	0
<i>Pseudopachychaeta approximatonervis</i> (Zetterstedt)	pseu_app	0	0	0	0	0	1	2	2	2	0	4	0
<i>Rhopalopterum carbonarium</i> (Loew)	rhop_car	0	7	0	0	3	18	87	3	19	2	4	4
<i>Rhopalopterum luteiceps</i> (Sabrosky)	rhop_lut	0	0	0	0	0	0	1	0	0	0	0	0
<i>Rhopalopterum painteri</i> (Sabrosky)	rhop_pai	6	4	0	3	0	1	25	0	0	0	0	0
<i>Rhopalopterum soror</i> (Macquart)	rhop_sor	0	0	0	0	0	0	1	0	0	0	1	1
<i>Rhopalopterum umbrosum</i> (Loew)	rhop_umb	1	0	0	0	4	0	109	2	11	1	3	0
<i>Speccafrons mallochi</i> (Sabrosky)	spec_mal	0	4	0	0	0	0	0	0	0	0	0	0
<i>Thaumatomyia glabra</i> (Meigen)	thau_gla	1	0	0	0	1	0	4	0	0	0	3	5
<i>Thaumatomyia grata</i> (Loew)	thau_gra	2	1	0	0	0	0	0	0	0	0	0	0
<i>Thaumatomyia pulla</i> (Adams)	thau_pul	0	0	0	0	0	0	0	0	0	2	0	0
<i>Thaumatomyia sp.1</i>	thau_sp1	0	0	3	0	0	0	0	0	0	0	0	0
<i>Tricimba melancholica</i> (Becker)	tric_mel	0	0	1	2	0	0	12	0	4	1	4	12
<i>Tricimba trisulcata</i> Adams	tric_tri	2	0	0	1	0	0	0	0	1	0	0	0
Milichiidae													
<i>Neophyllomyza gaulti</i> Brochu & Wheeler	neop_gaul	0	0	10	1	0	0	0	0	0	0	0	0
<i>Paramyia nitens</i> (Loew)	para_nite	0	0	1	0	0	0	0	0	0	1	3	2
Heleomyzidae													
<i>Allophyla atricornis</i> (Meigen)	allo_atri	1	0	0	0	0	0	0	0	0	0	0	0
<i>Suilla longipennis</i> (Loew)	suill_lon	6	0	0	0	0	0	0	0	0	0	0	0
Sphaeroceridae													
<i>Aptilotus nigriphallus</i> Marshall & Smith	apti_nig	0	0	1	0	0	0	0	0	0	0	0	0
<i>Coproica acutangula</i> (Zetterstedt)	copr_acut	0	0	2	1	0	0	0	0	2	2	0	1
<i>Coproica ferruginata</i> (Stenhammar)	copr_ferr	0	1	0	0	0	0	2	0	0	0	1	1
<i>Coproica hirtula</i> (Rondani)	copr_hirt	0	2	0	0	3	1	12	0	0	0	10	0
<i>Copromyza neglecta</i> (Malloch)	copr_neg	0	0	0	0	1	0	3	0	0	0	0	0
<i>Coproica sp.1</i>	copr_sp1	0	0	0	1	0	0	2	0	0	0	0	0
<i>Dahlimosina dahl</i> (Duda)	dahl_dah	0	0	0	1	0	0	0	0	1	0	0	2
<i>Elachisoma sp.</i>	elac_sp	0	0	0	0	0	0	1	0	0	0	0	0

<i>Ischiolepta intermedia</i> Han and Kim	isch_int	0	0	0	0	0	0	6	1	0	0	0	0
<i>Ischiolepta pusilla</i> (Fallén)	isch_pus	0	1	0	0	0	0	1	0	0	0	0	0
<i>Leptocera erythrocerca</i> (Becker)	lept_ery	93	219	162	0	4	59	13	0	9	15	5	9
<i>Limosininae</i> sp.1	limo_sp1	0	10	11	0	1	1	2	0	0	0	0	0
<i>Mesosphaerocera annulicornis</i> (Malloch)	meso_ann	0	0	0	3	0	0	0	0	0	0	0	3
<i>Minilimosina</i> ♀♀ spp.		1	0	0	1	0	0	1	0	0	0	0	0
<i>Minilimosina</i> sp.1	mini_sp1	0	0	1	0	0	0	0	0	0	0	0	0
<i>Minilimosina</i> sp.2	mini_sp2	0	1	0	0	0	0	0	0	0	0	0	0
<i>Opalimosina mirabilis</i> (Collin)	opal_mir	0	16	6	1	0	2	13	3	1	0	0	1
<i>Phthitia ovicercus</i> Marshall	phth_ove	0	0	0	0	0	0	3	0	0	0	0	0
<i>Phthitia plumosula</i> (Rondani)	phth_plu	0	12	0	0	0	0	0	0	0	0	0	0
<i>Phthitia quadricercus</i> Marshall	phth_qua	0	2	2	0	0	0	2	0	0	0	0	0
<i>Pseudocollinella</i> sp.1	pseu_sp1	0	41	1	0	0	0	0	0	0	0	0	0
<i>Pterogramma palliceps</i> (Jonhson)	pter_pall	17	4	22	4	0	0	0	0	0	1	0	0
<i>Pullimosina pullula</i> (Zettersdedt)	pull_pul	4	1	1	2	4	2	12	0	0	0	1	0
<i>Pullimosina</i> sp.1	pull_sp1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Rachispoda canadensis</i> Wheeler	rach_can	0	22	1	0	0	0	0	0	0	0	0	0
<i>Rachispoda frosti</i> (Malloch)	rach_fro	0	0	0	0	0	0	1	0	0	0	0	0
<i>Rachispoda limosa</i> (Fallén)	rach_lim	0	263	2	0	0	0	0	0	0	0	0	0
<i>Rachispoda</i> n.sp.1 TAW	rach_nsp1	0	6	0	0	0	0	0	0	0	0	0	0
<i>Rachispoda subpiligera</i> (Malloch)	rach_sub	0	6	6	1	0	1	0	0	0	0	0	0
<i>Spelobia brevipteryx</i> Marshall	spel_bre	0	0	0	0	0	0	0	0	0	0	0	1
<i>Spelobia frustrilabis</i> Marshall	spel_fru	0	5	4	1	0	0	1	0	0	0	0	3
<i>Spelobia luteilabris</i> (Rondani)	spel_lut	5	1	3	1	0	0	0	0	0	0	0	0
<i>Spelobia maculipennis</i> (Spuler)	spel_mac	1	0	0	0	1	0	30	0	0	0	0	0
<i>Spelobia ochripes</i> (Meigen)	spel_och	1	61	4	9	4	0	7	0	8	3	4	61
<i>Spelobia pappi</i> Roháček	spel_pap	0	0	1	0	0	0	27	0	0	0	0	0
<i>Spelobia semioculata</i> (Richards)	spel_sem	0	0	2	0	0	0	0	0	0	0	0	0
<i>Spelobia</i> sp.A	spel_spA	12	5	1	2	0	0	1	0	0	0	0	0
<i>Spelobia</i> sp.B	spel_spB	1	6	0	0	0	0	0	0	0	0	0	0
<i>Spelobia</i> sp.C	spel_spC	1	0	1	0	0	0	1	0	0	1	0	0
<i>Terrilimosina</i> sp.1	terr_sp1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Trachypella nuda</i> Roháček & Marshall	trac_nud	0	1	1	0	0	0	7	0	1	0	2	0
Diastatidae													
<i>Diastata pulchra</i> Loew	diast_pul	0	0	0	0	0	0	1	0	0	0	0	0
<i>Diastata</i> sp.1	diast_sp1	0	0	0	0	0	0	4	0	0	0	0	0
<i>Diastata</i> sp.2	diast_sp2	0	0	0	0	0	0	1	0	0	0	0	0
Drosophilidae													
<i>Chymomyza amoena</i> (Loew)	chym_amo	12	2	14	12	0	1	0	0	0	0	0	0
<i>Drosophila</i> (<i>Melanica</i> group) sp.1	droso_sp1	3	0	4	0	0	0	0	0	0	0	0	2
<i>Drosophila macrospina</i> Stalker & Spencer	droso_mac	20	7	9	26	0	0	0	0	0	0	0	1

<i>Drosophila nr. transversa</i> sp.	droso_sp18	5	1	0	2	0	0	0	0	0	0	0	1
<i>Drosophila putrida</i> Sturtevant	droso_put	4	1	0	7	0	0	0	0	0	0	0	3
<i>Drosophila quinaria</i> Loew	droso_qui	0	0	1	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.7	droso_sp7	6	0	1	3	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.9	droso_sp9	0	0	0	0	0	0	0	0	0	0	1	0
<i>Drosophila</i> sp.10	droso_sp10	0	7	0	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.11	droso_sp11	0	2	2	2	11	6	1	1	1	0	0	0
<i>Drosophila</i> sp.12	droso_sp12	0	0	1	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.13	droso_sp13	0	0	0	1	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.14	droso_sp14	0	0	0	1	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.15	droso_sp15	0	0	0	1	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.16	droso_sp16	0	0	2	0	0	0	0	0	0	0	0	0
<i>Drosophila testacea</i> Roser	droso_tes	25	2	0	16	0	0	0	0	0	0	0	6
<i>Drosophila transversa</i> Fallén	droso_tran	26	3	3	5	0	0	0	0	0	0	1	4
<i>Drosophila tripunctata</i> Loew	droso_tri	2	2	0	6	0	0	0	0	0	0	0	0
<i>Scaptomyza (Hemiscaptomyza) ?trochanterata</i> Collin	scap_tro	0	0	0	1	1	0	3	0	0	0	0	0
<i>Scaptomyza (Scaptomyza) flaveola</i> Meigen	scap_fla	0	2	0	16	0	0	0	0	0	0	0	0
<i>Scaptomyza adusta</i> (Loew)	scap_adu	0	0	0	0	1	0	3	0	0	0	2	1
<i>Scaptomyza pallida</i> (Zetterstedt)	scap_pal	32	2	11	0	3	16	4	0	0	1	9	3
Ephydriidae													
<i>Allotrichoma simplex</i> (Loew)	allo_sim	0	0	0	0	0	0	0	6	0	1	0	0
<i>Allotrichoma</i> ♀♀ spp.		0	0	0	0	0	0	0	15	5	2	0	0
<i>Athyroglossa granulosa</i> (Cresson)	athy_gra	2	5	56	3	0	3	0	0	0	0	0	0
<i>Axysta nigrifacies</i> Miyagi	axys_nigr	0	0	0	0	0	0	3	0	0	0	0	0
<i>Brachydeutera argentata</i> (Walker)	brac_arg	0	7	0	0	0	0	0	1	0	0	0	0
<i>Coenia curvicauda</i> (Meigen)	coen_cur	0	34	66	0	0	2	0	0	0	0	0	0
<i>Discocerina obscurella</i> (Fallén)	disc_obs	0	18	4	0	0	1	0	0	0	0	0	0
<i>Ditrichophora atrata</i> Cresson	ditr_atr	0	32	24	5	13	3	0	0	0	0	0	0
<i>Ditrichophora exigua</i> Cresson	ditr_exi	9	6	127	5	1	2	0	0	1	0	0	0
<i>Ditrichophora valens</i> Cresson	ditr_val	0	9	0	0	0	0	0	0	0	0	0	0
<i>Hyadina albovenosa</i> Coquillett	hyad_alb	0	0	0	0	0	0	0	0	0	0	1	2
<i>Hyadina vockerothi</i> Clausen	hyad_voc	0	0	0	0	0	0	1	0	0	0	0	0
<i>Hydrellia ?trichaeta</i> Cresson	hydr_tri	0	0	0	0	0	1	0	0	0	0	0	0
<i>Hydrellia americana</i> Cresson	hydr_ame	0	1	14	0	1	1	1	4	0	1	0	0
<i>Hydrellia griseola</i> (Fallén)	hydr_gri	1	4	0	4	1	6	0	5	0	0	0	0
<i>Hydrellia</i> sp.1	hydr_sp1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Hydrellia</i> sp.2	hydr_sp2	0	1	0	0	0	0	0	1	0	0	0	0
<i>Ilythea spilota</i> (Curtis)	ill_spil	0	2	3	0	0	0	0	0	0	0	0	0
<i>Nostima picta</i> (Fallén)	nost_pic	1	0	0	0	1	0	0	0	0	0	0	0
<i>Notiphila (Dichaeta) caudata</i> group		1	10	1	0	5	8	0	49	1	0	0	0
<i>Notiphila (Dichaeta) decoris</i> Williston	noti_dec	0	0	0	0	0	0	0	3	0	0	0	0

<i>Notiphila (Dichaeta) olivacea</i> Cresson	noti_oli	0	1	0	0	8	2	60	12	0	0	10	0
<i>Notiphila (Dichaeta) scalaris</i> Loew	noti_sca	0	0	0	0	4	0	11	17	0	0	7	0
<i>Notiphila (Dichaeta) sp.</i>	noti_sp	0	0	0	0	0	0	31	0	0	0	3	0
<i>Notiphila (Notiphila) avia</i> Loew	noti_avi	0	11	0	0	26	7	2	24	0	0	0	0
<i>Notiphila (Notiphila) nudipes</i> Cresson	noti_nud	0	0	0	0	0	0	0	1	0	0	0	0
<i>Notiphila (Notiphila) pauroura</i> Mathis	noti_pau	0	0	0	0	2	0	3	20	0	0	2	0
<i>Notiphila (Notiphila) phaeopsis</i> Mathis	noti pha	0	0	0	0	0	0	1	0	0	0	1	0
<i>Notiphila (Notiphila) solita</i> Walker	noti_soli	0	1	0	0	5	0	0	10	0	0	0	0
<i>Notiphila</i> ♀♀? <i>pauroura</i> Mathis		0	1	0	0	9	0	2	23	0	0	0	0
<i>Ochtera borealis</i> Clausen	ocht_bor	0	0	0	0	0	0	0	2	0	0	0	0
<i>Paracoenia (Paracoenia) fumosalis</i> Cresson	para_fum	0	0	0	0	0	0	0	35	0	0	0	0
<i>Parydra (Parydra) quadrituberculata</i> Loew	par_quad	0	3	2	0	0	1	0	0	0	0	0	0
<i>Parydra (Parydra)</i> ♀♀ spp.		0	1	2	0	0	0	0	0	0	0	0	0
<i>Philotelma alaskensis</i> Cresson	phil_ala	0	0	0	0	2	1	0	4	0	0	0	0
<i>Philygria debilis</i> Loew	phil_deb	0	0	0	0	0	0	0	0	1	0	1	1
<i>Platygympnopa helicis</i> Wirth	plat_hel	0	2	0	0	0	0	0	0	0	0	0	0
<i>Polytrichophora orbitalis</i> (Loew)	poly_orb	0	6	2	0	0	0	0	0	0	0	0	0
<i>Psilopa olga</i> Cresson	psil_olg	0	0	0	0	0	1	0	0	0	0	0	0
<i>Scatella (Scatella) stagnalis</i> Fallén	scat_sta	3	419	122	1	13	117	11	54	7	9	5	58
Calliphoridae													
<i>Lucilia coeruleiviridis</i> (Macquart)	luci_coe	0	2	0	1	0	0	0	0	0	0	0	0
<i>Lucilia illustris</i> (Meigen)	luci_ill	6	4	0	0	0	0	2	1	0	0	2	0
<i>Lucilia silvarium</i> Meigen	luci_sil	0	2	0	0	2	2	1	3	0	0	0	0
<i>Pollenia griseotomentosa</i> (Jacentkovsky)	poll_gri	1	1	1	0	0	1	0	0	0	0	0	0
<i>Pollenia labialis</i> Robineau-Desvoidy	poll_lab	8	0	2	5	0	0	0	0	0	0	0	0
<i>Pollenia pediculata</i> Macquart	poll_ped	2	13	2	0	2	0	1	0	0	1	2	1
<i>Pollenia rudis</i> (Fabricius)	poll_rud	0	0	0	0	0	0	0	0	0	0	1	0
Sarcophagidae													
<i>Blaesoxipha (Acridiophaga) hunteri</i> (Hough)	blae_hun	0	0	0	0	0	0	0	0	0	1	1	0
<i>Blaesoxipha (Acridiophaga) kyrtonidion</i> Pape	blae_kyr	0	0	0	0	0	0	0	0	0	2	0	0
<i>Blaesoxipha (Servaisia) uncata</i> (Wulp)	blae_unc	0	0	0	0	0	0	0	0	0	0	0	1
<i>Boettcheria bisetosa</i> Parker	boet_bis	0	0	0	1	0	0	0	0	0	0	1	0
<i>Boettcheria cimbici</i> s (Townsend)	boet_cim	3	1	0	0	0	0	0	0	0	4	16	24
<i>Boettcheria latisterna</i> Parker	boet_lat	0	0	0	0	0	0	0	0	0	0	1	3
<i>Brachicoma devia</i> (Fallén)	brac_dev	0	0	0	0	0	0	0	0	0	0	2	0
<i>Brachicoma sarcophagina</i> (Townsend)	bra_sarc	0	0	0	0	0	0	0	0	0	4	2	4
<i>Helicobia</i> ♀♀ spp.		0	0	0	0	0	0	0	0	1	0	2	1
<i>Helicobia rapax</i> (Walker)	heli_rap	0	0	0	0	0	0	0	0	0	1	4	3
<i>Helicobia stellata</i> (Wulp)	heli_ste	0	0	0	0	0	0	0	0	0	0	1	0
<i>Oxysarcodexia cingarus</i> (Aldrich)	oxys_cin	1	0	0	0	0	0	0	0	0	0	0	0
<i>Ravinia querula</i> (Walker)	ravi_que	0	0	0	0	0	0	0	0	0	1	1	1

<i>Ravinia stimulans</i> (Walker)	ravi_sti	0	0	1	0	0	0	1	0	0	1	9	5
<i>Sarcophaga (Robineauella) nearctica</i> Parker	sarc_nea	1	0	1	1	0	1	1	0	0	0	0	0
<i>Sarcophaga</i> sp.1	sarc_sp1	1	0	0	0	0	1	0	0	0	0	2	1
<i>Sarcophaga subvicina</i> Rohdendorf	sarc_sub	0	0	0	0	0	3	0	0	0	0	2	1
<i>Sarcophaginae</i> sp.1	sarca_sp1	6	0	1	0	0	0	0	0	0	0	0	1
<i>Sarcotachinella sinuata</i> (Meigen)	sarc_min	0	0	0	0	1	2	29	2	0	2	7	0
Scathophagidae													
<i>Chaetosa (Chaetosa) punctipes</i> Meigen	chaet_pun	0	0	0	0	0	0	0	1	0	0	0	0
<i>Scathophaga stercoraria</i> (Linnaeus)	scat_ste	0	0	0	0	0	0	0	0	0	0	0	1
	Total	536	1658	908	236	273	555	1044	339	244	198	294	468

Appendix 3.1. Abundance of Diptera species and morphospecies in the 15 bogs sites across the three ecoregions.

Species	Blainville	Pin-Rigide	Mirabel	Large Tea Field	Covey Hill	Ste-Jeanne d'Arc	Vauvert-Racine	Vauvert	Peribonka	Parc Nat. de la Pointe-Taillon	km 27	km 30	km 57	km 77	km 124
	MTL1	MTL2	MTL3	MTL4	MTL5	SAG1	SAG2	SAG3	SAG4	SAG5	BJM1	BJM2	BJM3	BJM4	BJM5
Platystomatidae															
<i>Riviella steyskali</i> Namba	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Tephritidae															
<i>Euaresta bella</i> (Loew)	1	2	4	18	0	0	0	0	0	0	0	0	0	0	0
<i>Paroxyna albiceps</i> (Loew)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Rhagoletis pomonella</i> (Walsh)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ulidiidae															
<i>Chaetopsis massyla</i> (Walker)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Chamaemyiidae															
<i>Leucopis americana</i> Malloch	0	0	0	1	6	2	1	2	0	1	6	9	0	0	1
<i>Leucopis maculata</i> Thompson	0	0	0	0	0	0	0	0	0	0	21	4	0	0	0
<i>Leucopis</i> (Ocellaris) sp.1	0	0	0	0	0	0	0	0	0	0	5	7	2	3	0
Lauxaniidae															
<i>Homoneura</i> (<i>Homoneura</i>) <i>pernotata</i> (Malloch)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Homoneura</i> (<i>Homoneura</i>) <i>philadelphica</i> (Macquart)	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0
<i>Homoneura</i> (<i>Tarsohomoneura</i>) <i>americana</i> (Wiedemann)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Homoneura</i> (<i>Tarsohomoneura</i>) <i>disjuncta</i> (Johnson)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Homoneura</i> (<i>Tarsohomoneura</i>) <i>houghii</i> (Coquillett)	0	0	1	2	0	0	7	0	0	0	0	0	0	0	0
<i>Homoneura</i> (<i>Tarsohomoneura</i>) <i>sheldoni</i> (Coquillett)	5	1	56	3	6	25	5	8	32	27	3	9	9	23	4
<i>Lauxania shewelli</i> Perusse & Wheeler	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
<i>Minettia</i> (<i>Minettia</i>) <i>cana</i> Melander	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
<i>Minettia</i> (<i>Minettia</i>) <i>lupulina</i> Fabricius	0	0	2	21	0	0	0	0	0	0	0	0	1	0	2
<i>Minettia lyraformis</i> Shewell	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Poecilolycia aspinosa</i> Shewell	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Poecilolycia browni</i> Curran	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sciomyzidae															
<i>Elgiva solicita</i> (Harris)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limnia boscii</i> (Robineau-Desvoidy)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Limnia conica</i> Steyskal	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pherbecta limenitis</i> Steyskal	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pteromicra leucothrix</i> Melander	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Tetanocera plebeja</i> Loew	0	0	0	0	0	4	0	0	0	7	1	0	0	1	0
<i>Tetanocera plumosa</i> Loew	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
<i>Tetanocera rotundicornis</i> Loew	0	0	0	0	0	8	0	0	0	7	0	0	0	0	1

<i>Tetanocera valida</i> Loew	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Dryomyzidae															
<i>Dryomyza anilis</i> Fallén	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sepsidae															
<i>Saltella sphondylii</i> (Schrank)	0	0	1	0	4	0	0	0	0	3	0	0	0	1	0
<i>Sepsis punctum</i> (Fabricius)	4	2	5	2	1	0	2	1	0	0	0	0	1	0	0
Agromyzidae															
<i>Amauromyza karli</i> Hendel	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerodontha (Cerodontha)dorsalis</i> s (Loew)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerodontha (Dizigomyza) magnicornis</i> Meigen	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerodontha (Icteromyza) churchillensis</i> Spencer	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
<i>Cerodontha (Poemyza) incisa</i> (Meigen)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Cerodontha longipennis</i> (Loew)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Liriomyza smilacinae</i> Spencer	0	0	0	0	0	0	0	0	0	0	11	4	4	2	4
<i>Liriomyza</i> sp.2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Melanagromyza</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Metopomyza interfrontalis</i> s (Melander)	0	5	1	0	1	1	0	5	1	2	0	2	0	0	0
<i>Phytomyza fuscula</i> Zetterstedt	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Anthomyzidae															
<i>Anthomyzidae</i> sp.1	0	1	0	0	0	0	0	0	0	0	4	1	0	0	0
<i>Mumetopia occipitalis</i> Melander	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Neoleria ?inscripta</i> (Meigen)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Clusiidae															
<i>Clusia lateralis</i> Walker	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Periscelididae															
<i>Cyamops halterata</i> Sabrosky	10	8	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyamops nebulosa</i> Melander	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Carnidae															
<i>Meoneura</i> sp.	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Meoneura vagans</i> (Fallén)	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0
Chloropidae															
<i>Apallates neocoxendix</i> (Sabrosky)	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0
<i>Apallates particeps</i> (Becker)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphanotrigonum</i> sp.1 TAW	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
<i>Aphanotrigonum trilineatum</i> (Meigen)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Chlorops</i> sp.3 TAW	46	49	11	0	10	14	4	16	1	5	0	8	0	1	1
<i>Chlorops</i> sp.4 TAW	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Chlorops</i> sp.5 TAW	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Chlorops</i> sp.6 TAW	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Conioscinella</i> sp.B	0	1	0	6	0	1	0	0	0	0	0	0	0	0	0
<i>Dasyopa</i> sp.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
<i>Dicraeus fennicus</i> Duda	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diplotoxa</i> sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Elachiptera costata</i> (Loew)	0	2	0	2	0	0	0	0	0	0	1	4	2	0	2

<i>Elachiptera nigriceps</i> (Loew)	1	0	3	0	0	0	0	0	0	0	0	0	0	0	
<i>Elachiptera vittata</i> Sabrosky	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1
<i>Epichlorops scaber</i> (Coquillett)	0	0	0	1	0	28	0	3	6	23	0	0	0	2	1
<i>Eribolus longulus</i> (Loew)	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hippelates plebejus</i> Loew	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Incertella bispina</i> (Malloch)	57	15	36	0	2	4	0	2	0	7	0	1	0	0	0
<i>Incertella incerta</i> (Becker)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Incertella minor</i> (Adams)	13	2	2	0	1	0	0	0	0	0	0	0	0	0	0
<i>Liohippелates bishoppi</i> (Sabrosky)	0	1	0	6	0	0	0	2	0	0	0	0	0	0	0
<i>Malloewia abdominalis</i> (Becker)	1	9	2	110	1	0	0	0	0	0	0	0	0	0	0
<i>Malloewia nigripalpis</i> (Malloch)	6	6	1	4	14	0	0	0	0	0	0	0	0	0	0
<i>Meromyza</i> sp.	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0
<i>Ocella parva</i> (Adams)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Ocella trigramma</i> Loew	0	0	2	7	0	0	0	0	0	0	0	0	0	0	0
<i>Oscinella</i> sp.1 TAW	0	0	1	23	0	0	0	0	0	0	0	0	0	0	0
<i>Oscinella</i> sp.2 TAW	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudopachychaeta approximatonervis</i> (Zetterstedt)	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudopachychaeta ruficeps</i> (Zetterstedt)	0	0	0	0	0	7	0	3	12	0	31	12	2	31	2
<i>Rhopalopterum atriceps</i> (Loew)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Rhopalopterum carbonarium</i> (Loew)	17	2	4	4	0	1	0	3	0	0	0	0	0	0	0
<i>Rhopalopterum soror</i> (Macquart)	0	0	1	1	0	0	1	1	0	0	1	4	0	2	0
<i>Rhopalopterum umbrosum</i> (Loew)	11	1	3	0	1	0	0	0	0	0	0	0	0	0	0
<i>Thaumatomyia glabra</i> (Meigen)	0	0	3	5	1	0	1	0	0	0	0	0	0	0	0
<i>Thaumatomyia pulla</i> (Adams)	0	2	0	0	0	0	0	0	1	0	36	44	55	149	98
<i>Tricimba cincta</i> Meigen	0	0	0	0	0	0	0	5	2	0	0	0	2	5	3
<i>Tricimba lineella</i> (Fallén)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Tricimba melancholica</i> (Becker)	4	1	4	12	9	5	4	3	10	3	35	32	16	18	34
<i>Tricimba</i> sp.1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
<i>Tricimba trisulcata</i> Adams	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Milichiidae															
<i>Neophyllomyza gaulti</i> Brochu & Wheeler	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Neophyllomyza quadricornis</i> Melander	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Paramyia nitens</i> (Loew)	0	1	3	1	1	0	18	2	135	0	0	1	0	1	0
Sphaeroceridae															
<i>Coproica acutangula</i> (Zetterstedt)	2	2	0	1	1	0	1	0	1	0	0	0	0	0	0
<i>Coproica ferruginata</i> (Stenhammar)	0	0	1	1	0	1	3	3	0	0	0	0	0	0	0
<i>Coproica hirtula</i> (Rondani)	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coproica</i> sp.1	0	0	0	0	0	0	10	14	0	1	0	0	3	0	0
<i>Copromyza neglecta</i> (Malloch)	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
<i>Dahlimosina dahli</i> (Duda)	1	0	0	2	0	8	4	4	2	0	0	0	2	3	5
<i>Gonioneura spinipennis</i> (Haliday)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Leptocera erythrocerca</i> (Becker)	9	14	4	9	5	2	10	3	3	6	1	11	2	1	1
<i>Lotophila</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Mesosphaerocera annulicornis</i> (Malloch)	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0

<i>Minilimosina</i> sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Minilimosina</i> sp.3	0	0	0	0	0	0	3	5	2	0	0	0	0	0
<i>Minilimosinae</i> sp.4	0	0	0	0	0	0	2	2	0	0	0	0	0	0
<i>Minilimosinae</i> sp.5	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Minilimosinae</i> sp.6	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Opalimosina mirabilis</i> (Collin)	1	0	0	1	1	1	6	43	1	1	0	1	0	0
<i>Phthitia ovicercus</i> Marshall	0	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Pterogramma palliceps</i> (Johson)	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pullimosina pullula</i> (Zettersdedt)	0	0	1	0	2	0	1	0	0	1	0	0	2	0
<i>Pullimosina</i> sp.1	0	0	0	0	0	0	0	0	0	0	5	1	0	0
<i>Pullimosina</i> sp.2	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Spelobia bifrons</i> (Stenhammar)	0	0	0	0	1	0	1	0	0	0	1	0	0	0
<i>Spelobia brevipteryx</i> Marshall	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Spelobia clunipes</i> (Meigen)	0	0	0	0	0	1	0	1	0	0	0	0	0	0
<i>Spelobia frustrilabis</i> Marshall	0	0	0	3	0	0	4	0	0	0	1	0	2	0
<i>Spelobia luteilabris</i> (Rondani)	0	0	0	0	0	0	7	4	0	0	0	0	8	0
<i>Spelobia ochripes</i> (Meigen)	8	3	4	61	3	0	7	2	1	1	0	0	0	0
<i>Spelobia pappi</i> Roháček	0	0	0	0	1	0	1	1	0	2	0	0	1	0
<i>Spelobia</i> sp.C	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spelobia</i> sp.D	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Spelobia</i> sp.E	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Terrilimosina</i> sp.1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Trachypella nuda</i> Roháček & Marshall	1	0	2	0	2	0	0	0	0	0	0	0	0	0
Drosophilidae														
<i>Drosophila macrospina</i> Stalker & Spencer	0	0	0	1	0	0	0	0	0	0	4	0	0	0
<i>Drosophila near transversa</i> AGT	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Drosophila putrida</i> Sturtevant	0	0	0	3	0	0	0	0	0	0	1	0	0	0
<i>Drosophila testacea</i> Roser	0	0	0	6	0	0	0	0	0	0	0	0	0	0
<i>Drosophila transversa</i> Fallén	0	0	1	4	0	0	3	3	0	0	7	3	0	2
<i>Drosophila (Melanica group)</i> sp.1	0	0	0	2	1	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Drosophila</i> sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.5	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Drosophila</i> sp.6	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Drosophila</i> sp.8	0	0	0	0	0	0	1	0	0	0	1	0	0	0
<i>Drosophila</i> sp.9	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Drosophila</i> sp.11	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scaptomyza adusta</i> (Loew)	0	0	2	1	1	0	0	0	0	0	1	1	0	1
<i>Scaptomyza flaveola</i> Meigen	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Scaptomyza pallida</i> (Zetterstedt)	0	1	9	3	1	1	0	0	0	0	9	8	1	18
Ephydridae														
<i>Allotrichoma bezzi</i> Becker	5	2	0	0	1	3	0	0	3	1	0	1	0	0

<i>Allotrichoma simplex</i> (Loew)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Ditrichophara exigua</i> Cresson	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hyadina albovenosa</i> Coquillett	0	0	1	2	0	0	0	0	0	0	0	0	0	0	
<i>Hydrellia americana</i> Cresson	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hydrellia griseola</i> (Fallén)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Notiphila (Dichaeta) olivacea</i> Cresson	0	0	10	0	0	0	0	0	0	0	0	0	0	0	
<i>Notiphila (Dichaeta) scalaris</i> Loew	0	0	7	0	0	0	0	0	0	0	0	0	0	0	
<i>Notiphila (Dichaeta)</i> sp.	0	0	3	0	0	0	0	0	0	0	0	0	0	0	
<i>Notiphila (Notiphila) pauroura</i> Mathis	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
<i>Notiphila (Notiphila) phaeopsis</i> Mathis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Philygria debilis</i> Loew	1	0	1	1	0	0	0	0	0	0	0	0	0	0	
<i>Polytrichophora orbitalis</i> (Loew)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Scatella (Scatella) stagnalis</i> Fallén	4	9	5	55	1	0	0	0	0	1	0	0	0	0	
Calliphoridae															
<i>Calliphora montana</i> (Shannon)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
<i>Cynomya cadaverina</i> Robineau-Desvoidy	0	0	0	0	0	0	4	7	1	1	2	8	8	1	4
<i>Lucilia illustris</i> (Meigen)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lucilia silvarium</i> Meigen	0	0	0	0	0	0	2	3	0	0	0	0	1	0	1
<i>Phormia regina</i> (Meigen)	0	0	0	0	0	0	2	19	1	0	0	0	1	0	0
<i>Pollenia pediculata</i> Macquart	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pollenia rudis</i> (Fabricius)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pollenia vagabunda</i> (Meigen)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sarcophagidae															
<i>Blaesoxipha (Acridiophaga) hunteri</i> (Hough)	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Blaesoxipha (Acridiophaga) kyrtonidion</i> Pape	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Blaesoxipha (Servaisia) coloradensis</i> Aldrich	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0
<i>Blaesoxipha (Servaisia) falciformis</i> Aldrich	0	0	0	0	0	3	1	2	0	0	0	0	0	4	6
<i>Blaesoxipha (Servaisia)</i> sp.1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Blaesoxipha (Servaisia) uncata</i> Wulp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Boettcheria bisetosa</i> Parker	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Boettcheria cimbicis</i> (Townsend)	0	4	16	24	2	7	8	12	7	3	0	2	1	2	14
<i>Boettcheria latisterna</i> Parker	0	0	1	3	0	3	2	5	6	0	2	1	0	0	0
<i>Brachicoma devia</i> (Fallén)	0	0	2	0	0	3	0	3	3	2	2	1	1	3	3
<i>Brachicoma sarcophagina</i> (Townsend)	0	4	2	4	2	0	0	0	0	0	0	0	0	0	0
<i>Fletcherimyia fletcheri</i> Aldrich	0	0	0	0	8	11	0	0	20	4	0	1	0	0	1
<i>Helicobia rapax</i> (Walker)	0	1	4	3	0	0	0	0	0	0	0	0	0	0	0
<i>Ravinia acerba</i> (Walker)	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
<i>Ravinia querula</i> (Walker)	0	1	1	1	0	0	2	1	2	0	0	0	0	0	0
<i>Ravinia stimulans</i> (Walker)	0	1	9	5	0	2	1	7	4	2	0	0	0	0	0
<i>Sarcophaga (Bercaeopsis) sarraceniae</i> Riley	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Sarcophaga (Neobellieria) bullata</i> (Parker)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Sarcophaga (Neobellieria) libera</i> Aldrich	0	0	0	0	0	0	0	1	0	0	0	0	4	0	0
<i>Sarcophaga (Robineauella) nearctica</i> Parker	0	0	0	0	0	0	5	7	0	0	0	0	2	0	0
<i>Sarcophaga (Wohlfahrtiopsis) utilis</i> Aldrich	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0

<i>Sarcophaga aldrichi</i> Parker	0	0	0	0	0	0	0	3	0	0	0	0	14	2	2
<i>Sarcophaga</i> sp.1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
<i>Sarcophaga subvicina</i> Rohdendorf	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
<i>Sarcophaginae</i> sp.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Sarcotachinella sinuata</i> (Meigen)	0	2	7	0	0	4	8	3	2	1	0	1	5	1	0
Scathophagidae															
<i>Cordilura (Cordilura) gagatina</i> Loew	0	0	0	0	0	0	0	0	0	0	5	0	3	0	0
<i>Cordilura (Cordilura) ontario</i> Curran	0	0	0	0	0	2	2	1	1	0	0	6	0	15	0
<i>Cordilura (Cordilurina) glabra</i> Loew	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
<i>Gonarticus</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Neochirosa</i> sp.	0	0	0	0	0	0	0	0	0	0	47	9	1	8	7
<i>Parallelomma vittata</i> (Meigen)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
<i>Scathophaga furcata</i> Say	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Scathophaga stercoraria</i> Linné	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Total	223	165	282	459	101	163	150	228	268	116	256	208	161	308	214

Appendix 3.2. Traits assigned to each Diptera species and morphospecies collected from the 15 bog sites in the three ecoregions. Refer to table 3.1 for an explanation of each trait and code (NA = unknown).

Species	Feeding	Size	SpeGen	Oviposit	Substrate	Range	Frequency	Rarity	Temp	Voltinism	Winter	Wetland
Platystomatidae												
<i>Riviella steyskali</i> Namba	PH	4.60	NA	NA	LL	1	1	R	45.3	NA	NA	NA
Tephritidae												
<i>Euaresita bella</i> (Loew)	PH	3.03	S	L	FL	1	2	C	48.7	U	A	F
<i>Paroxyna albiceps</i> (Loew)	PH	2.73	S	L	FL	1	1	R	45.3	U	A	F
<i>Rhagoletis pomonella</i> (Walsh)	PH	3.47	S	L	FL	1	1	R	45.3	U	A	F
Ulidiidae												
<i>Chaetopsis massyla</i> (Walker)	PH	5.00	G	T	P	1	1	R	45.5	M	P	A
Chamaemyiidae												
<i>Leucopis americana</i> Malloch	PR	2.53	G	T	I	3	3	C	52.8	M	P	F
<i>Leucopis maculata</i> Thompson	PR	1.83	S	T	I	1	2	C	42.7	M	P	F
<i>Leucopis (Ocellaris) sp.1</i>	PR	2.13	S	T	I	1	2	R	49.8	M	P	F
Lauxaniidae												
<i>Homoneura (Homoneura) pernotata</i> (Malloch)	SA	3.87	G	L	LL	1	1	R	45.3	M	L	I
<i>Homoneura (Homoneura) philadelphica</i> (Macquart)	SA	4.17	G	L	LL	2	2	R	48.5	M	L	I
<i>Homoneura (Tarsohomoneura) americana</i> (Wiedemann)	SA	3.67	G	L	LL	1	1	R	45.3	M	L	F
<i>Homoneura (Tarsohomoneura) disjuncta</i> (Johnson)	SA	2.80	G	L	LL	1	1	R	48.1	M	L	NA
<i>Homoneura (Tarsohomoneura) houghii</i> (Coquillett)	SA	3.27	G	M	LL	2	2	R	48.7	M	L	NA
<i>Homoneura (Tarsohomoneura) sheldoni</i> (Coquillett)	SA	3.07	G	M	LL	3	4	C	53.5	M	L	O
<i>Lauxania shewelli</i> Perusse & Wheeler	SA	4.05	G	L	LL	2	2	R	48.2	U	P	F
<i>Minettia (Minettia) cana</i> Melander	SA	3.40	G	M	LL	2	2	R	45.3	U	P	F
<i>Minettia (Minettia) lupulina</i> Fabricius	SA	3.60	G	M	LL	2	2	C	45.9	U	P	F
<i>Minettia lyraformis</i> Shewell	SA	4.00	G	M	LL	1	1	R	45.3	U	P	F
<i>Poecilolycia aspinosa</i> Shewell	SA	2.87	G	M	LL	1	1	R	45.3	NA	P	F
<i>Poecilolycia browni</i> Curran	SA	3.60	G	M	LL	1	1	R	45.3	NA	P	F
Sciomyzidae												
<i>Elgiva sollicita</i> (Harris)	PR	6.87	S	L	I	1	1	R	45.5	U	A	O
<i>Limnia boscii</i> (Robineau-Desvoidy)	PR	5.43	S	T	I	1	1	R	45.3	NA	NA	A
<i>Limnia conica</i> Steyskal	PR	4.00	S	L	I	1	1	R	41.8	NA	NA	O

<i>Pherbecta limenitis</i> Steyskal	PR	5.23	S	L	I	1	1	R	41.8	NA	NA	O
<i>Pteromicra leucothrix</i> Melander	PR	2.17	S	T	I	1	1	R	41.7	M	P	A
<i>Tetanocera plebeja</i> Loew	PR	7.92	S	L	I	2	2	R	52.3	M	P	O
<i>Tetanocera plumosa</i> Loew	PR	9.38	S	L	I	2	2	R	46	U	L	O
<i>Tetanocera rotundicornis</i> Loew	PA	7.77	S	T	I	1	2	R	52.3	M	P	O
<i>Tetanocera valida</i> Loew	PR	7.50	S	L	I	2	2	R	48.2	M	P	O
Dryomyzidae												
<i>Dryomyza anilis</i> Fallén	SA	6.92	G	L	C	1	1	R	45.3	NA	NA	F
Sepsidae												
<i>Saltella sphondylii</i> (Schrank)	SA	3.33	S	M	C	3	2	R	52.3	M	P	F
<i>Sepsis punctum</i> (Fabricius)	SA	4.17	G	M	C	3	3	R	52	M	L	F
Agromyzidae												
<i>Amauromyza karli</i> Hendel	PH	1.87	S	T	SB	1	1	R	45.7	M	P	F
<i>Cerodontha (Cerodontha)dorsalis</i> (Loew)	PH	2.27	G	T	LM	1	2	R	48.7	M	A	F
<i>Cerodontha (Dizigomyza) magnicornis</i> Meigen	PH	2.00	S	T	LM	1	1	R	45.5	M	A	F
<i>Cerodontha (Icteromyza) churchillensis</i> Spencer	PH	2.04	NA	T	LM	1	1	R	48.1	M	A	F
<i>Cerodontha (Poemyza) incisa</i> (Meigen)	PH	2.37	G	T	LM	1	1	R	48.1	M	A	F
<i>Cerodontha longipennis</i> (Loew)	PH	2.37	S	T	LM	1	1	R	40.6	M	A	F
<i>Liriomyza smilacinae</i> Spencer	PH	1.67	S	T	LM	1	2	C	49.8	M	P	F
<i>Liriomyza</i> sp.2	PH	1.87	S	T	LM	1	1	R	48.1	M	P	F
<i>Melanagromyza</i> sp.	PH	2.50	NA	T	SB	1	1	R	48.1	M	P	F
<i>Metopomyza interfrontalis</i> (Melander)	PH	1.40	S	T	LM	3	3	C	52.6	M	P	F
<i>Phytomyza fuscula</i> Zetterstedt	PH	1.67	G	T	LM	1	1	R	48.1	M	P	F
Anthomyzidae												
<i>Anthomyzidae</i> sp.1	NA	2.67	NA	M	NA	2	2	R	49.5	NA	NA	A
<i>Mumetopia occipitalis</i> Melander	NA	0.00	NA	M	NA	1	1	R	41.4	NA	NA	A
<i>Neoleria ?inscripta</i> (Meigen)	NA	0.00	NA	M	NA	1	1	R	40.6	NA	NA	A
Clusiidae												
<i>Clusia lateralis</i> Walker	SA	3.67	NA	M	RW	1	1	R	41.3	NA	P	F
Periscelididae												
<i>Cyamops halterata</i> Sabrosky	SA	2.57	NA	M	LL	1	2	C	48.7	U	L	A
<i>Cyamops nebulosa</i> Melander	SA	3.13	NA	M	LL	1	1	R	48.1	U	L	A
Carnidae												

<i>Meoneura</i> sp.	SA	1.08	G	T	S	2	2	R	41.8	NA	NA	F
<i>Meoneura vagans</i> (Fallén)	SA	1.50	G	T	S	2	2	R	52.7	NA	NA	NA
Chloropidae												
<i>Apallates neocoxendix</i> (Sabrosky)	SA	1.70	NA	NA	SI	2	2	R	49.6	M	NA	NA
<i>Apallates particeps</i> (Becker)	SA	1.67	NA	NA	SI	1	1	R	45.5	M	NA	F
<i>Aphanotrigonum</i> sp.1 TAW	SA	1.63	G	T	SI	1	1	R	41.4	M	A	F
<i>Aphanotrigonum trilineatum</i> (Meigen)	SA	2.53	G	T	SI	1	1	R	48.1	M	A	F
<i>Chlorops</i> sp.3 TAW	PH	2.77	S	M	SB	3	4	C	53.5	M	L	F
<i>Chlorops</i> sp.4 TAW	PH	1.57	G	T	SB	1	1	R	41.7	M	L	F
<i>Chlorops</i> sp.5 TAW	PH	2.25	S	M	SB	1	1	R	41.7	M	L	F
<i>Chlorops</i> sp.6 TAW	PH	3.21	G	T	SB	1	1	R	41.7	M	L	F
<i>Conioscinella</i> sp.B	SA	1.25	G	M	SI	2	2	R	48.6	NA	NA	NA
<i>Dasyopa</i> sp.	SA	1.33	NA	T	NA	1	1	R	45.3	M	NA	O
<i>Dicraeus fennicus</i> Duda	PH	1.80	S	M	FL	1	1	R	45.5	U	L	F
<i>Diplotoxa</i> sp.	PH	3.00	G	M	SB	1	1	R	48.1	NA	NA	NA
<i>Elachiptera costata</i> (Loew)	SA	2.57	G	T	SI	2	3	R	49.5	M	A	F
<i>Elachiptera nigriceps</i> (Loew)	SA	2.33	G	T	SI	1	2	R	48.6	M	A	F
<i>Elachiptera vittata</i> Sabrosky	SA	2.83	G	T	SI	1	2	R	48.8	M	A	F
<i>Epichlorops scaber</i> (Coquillett)	PH	3.07	NA	NA	SB	3	3	C	53.4	M	L	NA
<i>Eribolus longulus</i> (Loew)	SA	2.93	S	M	SI	1	1	R	45.5	M	A	F
<i>Hippelates plebejus</i> Loew	SA	2.00	G	M	C	1	2	R	45.5	M	NA	NA
<i>Incertella bispina</i> (Malloch)	PH	1.73	S	T	SI	3	3	C	52.8	M	L	F
<i>Incertella incerta</i> (Becker)	PH	1.42	S	T	SI	1	1	R	48.1	M	L	F
<i>Incertella minor</i> (Adams)	PH	1.40	S	T	SI	1	2	C	51.6	M	L	F
<i>Liohippelates bishoppi</i> (Sabrosky)	SA	1.93	NA	NA	C	2	2	R	49	M	NA	NA
<i>Malloewia abdominalis</i> (Becker)	SA	1.77	NA	NA	NA	1	2	C	51.6	M	NA	NA
<i>Malloewia nigripalpis</i> (Malloch)	SA	1.73	NA	NA	NA	1	2	C	51.6	M	NA	NA
<i>Meromyza</i> sp.	PH	3.33	G	NA	SB	2	2	R	48.9	M	L	F
<i>Ocella parva</i> (Adams)	PH	2.08	NA	NA	SI	1	1	R	48.1	NA	NA	F
<i>Ocella trigramma</i> Loew	PH	1.53	NA	NA	SI	1	2	R	45.4	M	L	NA
<i>Oscinella</i> sp.1 TAW	PH	1.67	G	T	SI	1	2	C	45.5	M	L	F
<i>Oscinella</i> sp.2 TAW	PH	1.53	G	T	SI	1	1	R	45.3	M	L	F
<i>Pseudopachychaeta approximatonervis</i> (Zetterstedt)	PH	1.87	S	M	FL	1	2	R	48.6	U	A	A

<i>Pseudopachychaeta ruficeps</i> (Zetterstedt)	PH	1.88	S	M	FL	3	3	C	53.5	U	A	A
<i>Rhopalopterum atriceps</i> (Loew)	SA	1.75	G	NA	SI	1	1	R	41.4	M	L	A
<i>Rhopalopterum carbonarium</i> (Loew)	PH	2.03	G	NA	SI	2	3	C	52	M	L	A
<i>Rhopalopterum soror</i> (Macquart)	PH	1.50	G	NA	SI	3	3	R	52.8	M	L	A
<i>Rhopalopterum umbrosum</i> (Loew)	PH	1.97	G	NA	SI	1	2	R	51.6	M	L	A
<i>Thaumatomyia glabra</i> (Meigen)	PR	2.23	S	T	I	2	2	R	48.7	M	A	F
<i>Thaumatomyia pulla</i> (Adams)	PR	1.93	S	T	I	3	3	C	53.5	M	A	F
<i>Tricimba cincta</i> Meigen	SA	2.08	G	M	SI	2	2	R	52	M	A	F
<i>Tricimba lineella</i> (Fallén)	SA	1.50	G	M	SI	1	2	R	49.1	M	A	F
<i>Tricimba melancholica</i> (Becker)	SA	1.83	G	M	SI	3	4	C	53.5	M	A	F
<i>Tricimba</i> sp.1	SA	1.83	G	M	SI	2	2	R	49.7	M	A	F
<i>Tricimba trisulcata</i> Adams	SA	2.20	G	M	SI	1	1	R	41.8	M	A	F
Milichiidae												
<i>Neophyllomyza gaulti</i> Brochu & Wheeler	SA	1.77	S	M	RW	1	1	R	48.2	U	NA	F
<i>Neophyllomyza quadricornis</i> Melander	SA	1.67	S	M	RW	1	1	R	46	NA	NA	F
<i>Paramyia nitens</i> (Loew)	SA	1.80	G	M	I	3	3	C	49.8	NA	NA	F
Sphaeroceridae												
<i>Coproica acutangula</i> (Zetterstedt)	SA	1.93	G	T	C	2	3	R	52.7	NA	NA	F
<i>Coproica ferruginata</i> (Stenhammar)	SA	1.77	G	T	C	2	2	R	48.9	NA	NA	F
<i>Coproica hirtula</i> (Rondani)	SA	1.27	G	T	C	1	1	R	45.5	NA	NA	F
<i>Coproica</i> sp.1	SA	1.37	G	T	C	2	2	C	52.7	NA	NA	F
<i>Copromyza neglecta</i> (Malloch)	SA	3.23	G	T	C	1	2	R	52.3	M	A	F
<i>Dahlimosina dahli</i> (Duda)	SA	1.20	G	M	RW	3	3	C	52	NA	NA	O
<i>Gonioneura spinipennis</i> (Haliday)	SA	1.58	G	T	C	1	1	R	48	NA	NA	NA
<i>Leptocera erythrocerca</i> (Becker)	SA	2.33	G	M	RW	3	4	C	53.5	M	P	F
<i>Lotophila</i> sp.	SA	2.08	G	NA	C	1	1	R	48.1	NA	NA	NA
<i>Mesosphaerocera annulicornis</i> (Malloch)	SA	3.13	NA	NA	NA	1	1	R	45.3	NA	NA	NA
<i>Minilimosina</i> sp.1	SA	1.33	G	M	RW	1	1	R	48.1	NA	NA	F
<i>Minilimosina</i> sp.3	SA	1.50	G	M	RW	1	2	R	49	NA	NA	F
<i>Minilimosinae</i> sp.4	SA	1.42	G	M	RW	1	2	R	48.1	NA	NA	F
<i>Minilimosinae</i> sp.5	SA	1.17	G	M	RW	1	1	R	48.1	NA	NA	F
<i>Minilimosinae</i> sp.6	SA	1.42	G	M	RW	1	1	R	48	NA	NA	F
<i>Opalimosina mirabilis</i> (Collin)	SA	1.60	S	T	C	3	3	C	53.5	NA	NA	F

<i>Phthitia ovicercus</i> Marshall	SA	1.47	G	M	S	1	1	R	48.1	NA	NA	O
<i>Pterogramma palliceus</i> (Johson)	SA	1.77	G	NA	RW	1	1	R	45.7	NA	NA	F
<i>Pullimosina pullula</i> (Zettersdedt)	SA	1.93	G	M	RW	3	3	R	52.7	NA	NA	O
<i>Pullimosina</i> sp.1	SA	1.53	G	M	RW	1	2	R	49.1	NA	NA	O
<i>Pullimosina</i> sp.2	SA	1.50	G	M	RW	1	2	R	48.1	NA	NA	O
<i>Spelobia bifrons</i> (Stenhammar)	SA	1.79	S	M	C	3	2	R	51.6	NA	NA	O
<i>Spelobia brevipteryx</i> Marshall	SA	1.73	G	T	C	1	1	R	45.3	NA	NA	F
<i>Spelobia clunipes</i> (Meigen)	SA	1.75	G	NA	S	1	2	R	48.3	M	A	F
<i>Spelobia frustrilabis</i> Marshall	SA	1.90	G	M	C	1	1	R	45.3	NA	NA	F
<i>Spelobia luteilabris</i> (Rondani)	SA	1.92	S	T	C	2	2	C	51.3	M	A	F
<i>Spelobia ochripes</i> (Meigen)	SA	2.33	S	M	RW	2	3	C	53.4	M	A	F
<i>Spelobia pappi</i> Roháček	SA	2.13	G	M	C	1	1	R	48.1	M	A	O
<i>Spelobia</i> sp.C	SA	1.87	G	NA	C	1	1	R	45.7	NA	NA	NA
<i>Spelobia</i> sp.D	SA	1.75	G	NA	C	1	1	R	48.1	M	A	NA
<i>Spelobia</i> sp.E	SA	2.33	G	NA	C	1	1	R	46	M	A	NA
<i>Terrilimosina</i> sp.1	SA	1.40	G	M	RW	1	2	R	48.5	NA	NA	F
<i>Trachyopella nuda</i> Roháček & Marshall	SA	1.60	G	T	RW	1	2	R	51.6	NA	NA	A
Drosophilidae												
<i>Drosophila macrospina</i> Stalker & Spencer	NA	2.40	NA	NA	NA	2	2	R	48.2	NA	A	NA
<i>Drosophila near transversa</i> AGT	SA	2.50	G	M	RW	1	1	R	45.3	M	A	F
<i>Drosophila putrida</i> Sturtevant	SA	2.53	G	M	RW	2	2	R	48.2	M	A	F
<i>Drosophila testacea</i> Roser	SA	2.33	G	M	RW	1	1	R	45.3	M	A	F
<i>Drosophila transversa</i> Fallén	SA	2.50	G	M	RW	3	3	C	52.8	M	A	F
<i>Drosophila (Melanica</i> group) sp.1	NA	2.83	NA	NA	NA	1	2	R	48.5	NA	A	NA
<i>Drosophila</i> sp.2	NA	2.21	NA	NA	NA	1	2	R	40.6	NA	A	NA
<i>Drosophila</i> sp.3	NA	2.50	NA	NA	NA	1	1	R	45.6	NA	A	NA
<i>Drosophila</i> sp.4	NA	2.58	NA	NA	NA	1	1	R	45.6	NA	A	NA
<i>Drosophila</i> sp.5	NA	2.58	NA	NA	NA	2	2	R	49	NA	A	NA
<i>Drosophila</i> sp.6	NA	1.83	NA	NA	NA	1	1	R	46	NA	A	NA
<i>Drosophila</i> sp.8	NA	2.83	NA	NA	NA	2	2	R	51.6	NA	A	NA
<i>Drosophila</i> sp.9	NA	1.47	NA	NA	NA	1	1	R	45.5	NA	A	NA
<i>Drosophila</i> sp.11	NA	3.17	NA	NA	NA	1	1	R	41.8	NA	A	NA
<i>Scaptomyza flaveola</i> Meigen	PH	1.54	NA	T	LM	1	1	R	48.1	M	P	NA

<i>Scaptomyza adusta</i> (Loew)	PH	2.33	G	T	LM	2	3	R	52.4	M	P	NA
<i>Scaptomyza pallida</i> (Zetterstedt)	PH	2.17	S	T	FL	3	3	C	52.4	M	P	F
Ephydriidae												
<i>Allotrichoma bezzi</i> Becker	SA	1.79	G	M	C	3	3	R	53.5	NA	NA	F
<i>Allotrichoma simplex</i> (Loew)	SA	1.83	G	M	C	2	2	R	45.7	NA	NA	F
<i>Ditrichophara exigua</i> Cresson	SA	1.70	NA	L	S	1	1	R	41.8	NA	NA	NA
<i>Hyadina albovenosa</i> Coquillett	SA	1.37	S	L	SB	1	2	R	45.5	NA	NA	F
<i>Hydrellia americana</i> Cresson	PH	1.40	G	L	LM	1	1	R	45.7	NA	L	F
<i>Hydrellia griseola</i> (Fallén)	PH	2.27	G	L	LM	1	1	R	41.4	NA	L	F
<i>Notiphila (Dichaeta) olivacea</i> Cresson	SA	5.00	S	L	S	1	1	R	45.5	M	L	O
<i>Notiphila (Dichaeta) scalaris</i> Loew	SA	4.13	S	L	S	1	1	R	45.5	M	L	O
<i>Notiphila (Dichaeta)</i> sp.	SA	4.13	S	L	S	1	1	R	45.5	M	L	O
<i>Notiphila (Notiphila) paouroura</i> Mathis	SA	3.67	S	L	S	1	1	R	45.5	M	L	O
<i>Notiphila (Notiphila) phaeopsis</i> Mathis	SA	3.40	S	L	S	1	1	R	45.5	M	L	O
<i>Philygria debilis</i> Loew	PH	1.40	NA	L	NA	1	2	R	48.6	NA	NA	F
<i>Polytrichophora orbitalis</i> (Loew)	SA	1.97	NA	L	S	1	1	R	48.1	NA	NA	F
<i>Scatella (Scatella) stagnalis</i> Fallén	SA	2.00	G	L	S	2	3	C	51.6	NA	NA	F
Calliphoridae												
<i>Calliphora montana</i> (Shannon)	SA	4.54	G	T	C	1	1	R	48	M	NA	F
<i>Cynomya cadaverina</i> Robineau-Desvoidy	SA	10.63	G	T	C	2	3	C	53.5	M	NA	F
<i>Lucilia illustris</i> (Meigen)	SA	8.13	G	T	C	1	1	R	45.5	M	L	F
<i>Lucilia silvarium</i> Meigen	PA	6.88	G	T	A	2	2	R	48.3	M	L	F
<i>Phormia regina</i> (Meigen)	SA	10.08	G	T	C	1	2	C	51.3	M	A	F
<i>Pollenia pediculata</i> Macquart	PA	8.21	S	M	I	1	1	R	45.7	M	A	F
<i>Pollenia rudis</i> (Fabricius)	PA	8.33	S	M	I	1	1	R	45.5	M	A	F
<i>Pollenia vagabunda</i> (Meigen)	PA	7.50	S	M	I	1	1	R	48	M	A	F
Sarcophagidae												
<i>Blaesoxipha (Acridiophaga) hunteri</i> (Hough)	PA	6.25	S	T	I	1	2	R	45.7	M	P	F
<i>Blaesoxipha (Acridiophaga) kyrtonidion</i> Pape	PA	6.67	S	T	I	2	2	R	49	M	P	F
<i>Blaesoxipha (Servaisia) coloradensis</i> Aldrich	PA	7.92	S	T	I	2	2	R	53.5	M	P	F
<i>Blaesoxipha (Servaisia) falciformis</i> Aldrich	PA	6.88	S	T	I	2	2	R	49	M	P	F
<i>Blaesoxipha (Servaisia)</i> sp.1	PA	8.13	S	T	I	1	1	R	41.7	M	P	F
<i>Blaesoxipha (Servaisia) uncata</i> Wulp	PA	8.33	S	T	I	1	1	R	45.3	M	P	F

<i>Boettcheria bisetosa</i> Parker	SA	10.42	G	T	I	1	1	R	45.5	M	P	F
<i>Boettcheria cimbicis</i> (Townsend)	PA	7.92	G	T	I	3	4	C	53.5	U	P	F
<i>Boettcheria latisterna</i> Parker	PA	8.75	G	T	I	3	3	R	53.5	U	P	F
<i>Brachicoma devia</i> (Fallén)	PA	7.50	G	T	I	3	3	C	53.5	M	P	F
<i>Brachicoma sarcophagina</i> (Townsend)	PA	6.96	G	T	I	1	2	R	48.6	M	P	F
<i>Fletcherimyia fletcheri</i> Aldrich	SA	8.54	G	L	I	3	3	C	53.5	U	P	O
<i>Helicobia rapax</i> (Walker)	PA	4.54	G	T	I	1	2	R	45.7	M	P	F
<i>Ravinia acerba</i> (Walker)	SA	8.75	G	T	C	1	2	R	48.3	M	P	F
<i>Ravinia querula</i> (Walker)	SA	10.21	G	T	C	2	3	R	49.7	M	P	F
<i>Ravinia stimulans</i> (Walker)	SA	7.08	G	T	C	2	3	C	53.4	M	P	F
<i>Sarcophaga (Bercaeopsis) sarraceniae</i> Riley	SA	11.67	G	M	I	1	1	R	48.1	M	P	O
<i>Sarcophaga (Neobellieria) bullata</i> (Parker)	SA	10.00	G	T	C	1	1	R	48	M	P	F
<i>Sarcophaga (Neobellieria) libera</i> Aldrich	SA	11.67	G	T	C	2	2	R	51.3	M	P	F
<i>Sarcophaga (Robineauella) nearctica</i> Parker	SA	10.42	S	T	C	2	2	R	51.3	M	P	F
<i>Sarcophaga (Wohlfahrtiopsis) utilis</i> Aldrich	PA	11.04	S	T	M	1	2	R	48.3	M	P	F
<i>Sarcophaga aldrichi</i> Parker	PA	10.42	S	T	I	2	2	C	51.3	M	P	F
<i>Sarcophaga</i> sp.1	SA	9.38	NA	T	C	1	2	R	45.5	M	P	F
<i>Sarcophaga subvicina</i> Rohdendorf	SA	10.00	S	T	C	1	2	R	45.5	M	P	F
<i>Sarcophaginae</i> sp.1	NA	7.50	NA	T	NA	1	1	R	45.3	M	P	F
<i>Sarcotachinella sinuata</i> (Meigen)	PA	6.67	S	T	I	3	3	C	53.5	M	P	F
Scathophagidae												
<i>Cordilura (Cordilura) gagatina</i> Loew	PH	5.83	S	M	SB	1	2	R	41.7	U	P	A
<i>Cordilura (Cordilura) ontario</i> Curran	PH	6.79	S	M	SB	2	3	C	53.5	U	P	A
<i>Cordilura (Cordilurina) glabra</i> Loew	PH	8.75	S	M	SB	1	1	R	41.4	U	P	A
<i>Gonarcticus</i> sp.	PH	5.83	S	T	LM	1	2	R	41.7	NA	NA	F
<i>Neochiroso</i> sp.	PH	5.13	S	T	LM	1	2	C	49.8	NA	NA	F
<i>Parallelomma vittata</i> (Meigen)	PH	4.50	G	T	LM	1	2	R	41.7	M	P	F
<i>Scathophaga furcata</i> Say	SA	6.50	G	T	C	1	1	R	41.7	M	A	F
<i>Scathophaga stercoraria</i> Linné	SA	7.33	G	T	C	1	1	R	45.3	M	A	F

Appendix 3.3. Coordinates, local variables, landscape variables and climate variables in the 15 bog sites across the three ecoregions. Water table level was determined following these categories: 1. Water level below surface, 2. Water level at surface, 3. Water level above surface.

	MTL1	MTL2	MTL3	MTL4	MTL5	SAG1	SAG2	SAG3	SAG4	SAG5	BJM1	BJM2	BJM3	BJM4	BJM5
Latitude	45.70	45.10	45.68	45.12	45.01	48.88	48.74	48.77	48.75	48.69	49.83	49.83	49.96	50.14	50.48
Longitude	-73.83	-73.87	-74.04	-74.22	-73.82	-72.17	-72.26	-72.15	-71.96	-71.96	-77.31	-77.27	-77.12	-77.09	-77.29
Local variables															
Tree cover (%)	1	20	1	25	5	15	5	5	30	1	15	10	30	30	40
Water above surface (%)	0	10	0	0	0	0	0	0	0	0	0	0	10	0	0
Water table level	2	2	1	1	2	1	1	1	1	2	1	1	2	1	1
Fluctuation (cm)	4	0	0	0	0	0.8	7	6.2	10.5	2.4	3.5	0.4	4	5.5	4.8
pH	4.4	5.1	4.7	3.7	4.4	3.8	3.4	3.0	3.3	3.6	3.9	3.7	3.7	3.7	4.0
Soil temperature (°C)	23.8	23.1	24.9	19.7	23.9	19.9	15.8	20.1	16.0	17.6	16.2	18.4	15.6	15.5	12.4
Conductivity (µS/m)	28.0	93.5	31.0	81.0	32.5	46.2	70.3	125.2	67.5	42.6	47.9	50.8	63.0	69.6	81.4
<i>Andromeda glaucophylla</i>	0	0	0	0	3	1.4	19	1.4	0	0	1	15.2	15.2	12	9.4
<i>Betula populifolia</i>	0	4	0	6	1	0	0	0	0	0	0	0	0	0	0
<i>Carex magellanica</i>	0	0	0	0	0	0	0	0	0	0	7.8	0	0	0	7.4
<i>Carex oligosperma</i>	69	52	0	0	22	30	0	29	3	8	0	20	20	0	0
<i>Carex pauciflora</i>	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
<i>Carex stricta</i>	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
<i>Chamaedaphne calyculata</i>	47	25	4	0	56	34	65	36	48	57	40	21.6	21.6	55	50
<i>Cladonia</i> spp.	0	0	0	3	0	0	1	0	2	0	0	0	0	0	0
<i>Drosera rotundifolia</i>	21	0	0	0	6.4	2	0	0	1	0.2	0	0	0	0	0

<i>Equisetum sylvaticum</i>	0	0	0	0	0	0	0	0	0	0	4.8	0	0	0	0
<i>Eriophorum vaginatum</i>	3	0	9	2.4	0	13	0	0	8	42	4.6	17	17	8.4	26
<i>Eriophorum viridicarinatum</i>	0	0	0	0	0	9	0	1	0	0	0	0	0	0	0
<i>Kalmia angustifolia</i>	0	0	60	29	6	28	23	10	14	6	1	0.4	0.4	1	1
<i>Larix laricina</i>	0	0	6	0	0	5	0	0	0	2	0	1	1	0	0
<i>Ledum groenlandicum</i>	0	0	11	0	0	16	4	6	17	0	27	22	22	28	26
litter	0	13	21	55	6	8.4	27	13.4	33	10	4.2	19.4	19.4	22.6	21
<i>Lysimachia terrestris</i>	0	12.4	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Maianthemum trifolium</i>	0	0	0	0	59	0	0	0	1	0	35	13.6	13.6	15.6	44
Open pool	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0
<i>Picea mariana</i>	0	0	0	0	0	5	0	0	21	0	1	23	23	8.4	21
<i>Polytrichum</i> spp.	17	10	66	47	15	32.4	0	61	0	7	13.2	3	3	0	8.2
<i>Rubus Chamaemorus</i>	0	0	0	0	0	0	0	0	0	0	0	1.6	17.4	1.2	11.4
<i>Salix pedicellaris</i>	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0
<i>Salix pyrifolia</i>	0	17	0	0	0	0	0	0	0	0	10	0	0	0	0
<i>Sarracenia purpurea</i>	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0
<i>Sphagnum</i> spp.	67	100	91	20	100	99	76	84	100	99	99.6	90	90	100	100
<i>Spiraea alba</i>	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium ?angustifolium</i>	0	0	28	0	0	0	0	0	0	0	1.2	1	1	3	0
<i>Vaccinium myrtilloides</i>	0	0	0	53	0	0	0	0	0	0	0	3	3	0	0
<i>Vaccinium oxycoccos</i>	0	0	0	0	14	4	0	0	5.4	9	3.8	19.2	19.2	8	17

Landscape variables																
Open water (%)	0.2	1.4	0.5	0.0	0.9	0.1	11.2	0.7	13.2	7.5	5.9	0.1	0.9	0.0	0.0	
Exposed land (%)	5.0	9.0	9.4	4.5	1.9	4.8	0.0	0.1	0.5	0.0	1.1	1.0	2.4	0.3	0.9	
Urban development (%)	17.5	1.4	18.3	0.4	1.4	3.3	0	0	0	0	0	0	0.2	0	0	
Low vegetation (%)	8.2	6.0	9.4	4.4	4.8	14.1	0.3	23.2	2.3	0.6	15.6	4.3	8.2	9.6	7.6	
Wetlands (%)	9.3	20.5	5.4	39.1	4.1	50.3	44.2	28.6	41.6	51.4	3.6	8.3	19.1	3.5	5.3	
Agriculture (%)	9.2	22.4	34.3	25.1	13.0	0.2	0	7.6	11.6	0	0	0	0	0	0	
Forest (%)	50.6	39.3	22.7	26.5	74.0	27.2	44.3	39.8	30.8	40.5	73.8	86.3	69.4	86.6	86.2	
Area (ha)	65.3	16.6	67.52	161.6	55.1	1863	1960	1711	1199	3780	19.9	62.8	20.4	8.4	7.7	
Climate variables																
Annual Mean Temp (°C)	5.7	6.5	5.6	6.4	5.5	1.9	2.3	2	2	2.2	-0.3	-0.3	-0.5	-0.6	-1.2	
Temp Seasonality (sd *100) (°C)	10776	10472	10738	10499	10323	11870	11859	11833	11739	11726	12317	12316	12374	12351	12444	
Max Temp of Warmest Month (°C)	26.2	26.9	26	27	25.5	23.2	23.5	23.2	23.1	23.1	22.7	22.7	22.5	22.2	21.6	
Min Temp of Coldest Month (°C)	-15.6	-14.4	-15.7	-14.4	-15.1	-22.8	-22.1	-22.5	-22.4	-22.2	-25.4	-25.4	-25.6	-25.8	-26.5	
Mean Temp of Warmest Quarter (°C)	18.9	19.4	18.8	19.3	18.2	16.1	16.5	16.2	16	16.2	14.5	14.5	14.4	14.2	13.6	
Mean Temp of Coldest Quarter (°C)	-9	-7.7	-9	-7.8	-8.5	-14.7	-14.3	-14.5	-14.4	-14.2	-17.3	-17.3	-17.6	-17.7	-18.5	
Annual Precipitation (mm)	968	892	958	924	912	838	822	829	846	844	882	887	888	876	869	

Appendix 3.4. Ground cover variables reduced with principal component analysis. Principal components (PC) 1 to 5 were identified as significant using the Kaiser-Guttman criterion (Yeomans and Golder 1982). Variables with the largest loadings are in bold and were forming the clusters of interest.

Substrate cover	PC1	PC2	PC3	PC4	PC5
<i>Andromeda glaucophylla</i>	-0.17	-0.08	-0.03	0.06	0.02
<i>Betula populifolia</i>	0.08	-0.01	0.05	0.09	-0.01
<i>Carex oligosperma</i>	0.06	0.44	0.14	-0.01	0.13
<i>Carex stricta</i>	0.00	-0.02	-0.14	0.07	0.00
<i>Chamaedaphne calyculata</i>	-0.23	0.18	-0.19	0.03	-0.02
<i>Cladonia</i> spp.	0.04	-0.05	-0.02	0.05	0.03
<i>Drosera rotundifolia</i>	0.02	0.15	0.02	-0.01	0.00
<i>Eriophorum vaginatum</i>	-0.12	-0.09	0.07	-0.15	0.15
<i>Eriophorum viridi-carinatum</i>	0.02	0.02	-0.01	-0.06	0.02
<i>Kalmia angustifolia</i>	0.23	-0.19	-0.16	-0.10	0.00
<i>Larix laricina</i>	0.02	-0.02	0.00	-0.10	0.04
<i>Ledum groenlandicum</i>	-0.22	-0.16	0.01	-0.13	0.00
litter	0.07	-0.23	-0.03	0.11	0.08
<i>Lysimachia terrestris</i>	0.03	0.07	0.01	0.06	0.00
<i>Maianthemum trifolium</i>	-0.30	-0.07	0.18	0.04	-0.24
<i>Picea mariana</i>	-0.23	-0.11	0.10	-0.03	0.15
<i>Polytrichum</i> spp.	0.35	0.03	0.13	-0.17	-0.13
<i>Salix pedicellaris</i>	0.13	-0.10	0.07	0.09	0.01
<i>Salix pyrifolia</i>	0.00	0.07	0.02	0.06	-0.08
<i>Sarracenia purpurea</i>	-0.01	0.00	0.00	0.01	-0.01
<i>Sphagnum</i> spp.	-0.14	0.10	-0.08	-0.07	-0.02
<i>Spiraea alba</i>	0.03	0.07	0.01	0.06	0.00
<i>Vaccinium ?angustifolium</i>	0.02	-0.08	-0.01	-0.12	-0.05
<i>Vaccinium myrtilloides</i>	0.17	-0.17	0.15	0.13	0.06
<i>Vaccinium oxycoccos</i>	-0.22	-0.05	0.11	-0.03	0.04