

Population ecology and community structure of mosquitoes (Diptera:
Culicidae) across multiple periurban habitats in the West Island
of Montreal, Quebec, Canada

Christopher A. Cloutier

Department of Natural Resource Sciences
McGill University
Montreal, Quebec, Canada

December 2016

A thesis submitted to McGill University in partial fulfillment of the requirements of the
degree of Master of Science

© Christopher Cloutier 2016

Table of Contents

Abstract	...5
Résumé	...6
List of Tables	...8
List of Figures	...9
Thesis Format	...11
Acknowledgements	...11
Contribution of Authors	...12
Chapter 1: Introduction and Literature Review	...13
1.1 Introduction	...13
1.1.1 Thesis rationale	...13
1.1.2 Research objectives	...13
1.2 Mosquito research in North America	...15
1.3 Effect of habitat on mosquito communities	...18
1.4 Effect of environmental variables on mosquito communities	...21
1.5 Sampling mosquitoes	...24
1.6 Modeling mosquito populations	...25
1.7 New technology for mosquito taxonomy and monitoring	...27
1.8 References	...28
1.9 Connecting statement	...43
Chapter 2: The diversity and community structure of mosquitoes (Diptera: Culicidae) in suburban, field, and forest habitats in Montréal (Canada)	...44
2.1 Introduction	...44
2.2 Methods	...46
2.2.1 Study sites	...46
2.2.2 Sample collection and specimen processing	...46
2.2.3 Trapping considerations	...47
2.2.4 Data analyses	...47

2.3 Results	...49
2.3.1 General results	...49
2.3.2 Community structure	...50
2.3.3 Abundance and richness	...50
2.3.4 Shared species	...51
2.3.5 Relative abundance of selected species	...51
2.4 Discussion	...52
2.4.1 Habitat in shaping community structure	...53
2.4.2 Abundance	...54
2.4.3 Richness	...55
2.4.4 Shared species	...56
2.4.5 Relative abundance of selected species	...57
2.4.6 Vector ecology	...59
2.4.7 Conclusions	...59
2.5 References	...60
2.6 Tables and Figures	...70
2.7 Connecting Statement	...76
Chapter 3: The effect of temperature and precipitation on the phenology and abundance of mosquito (Culicidae) communities in suburban, field and forested habitats in Montreal (Canada)	...77
3.1 Introduction	...77
3.2 Methods	...78
3.2.1 Study site	...78
3.2.2 Sample collection and specimen processing	...79
3.2.3 Environmental data	...80
3.2.4 Data analyses	...80
3.3 Results	...82
3.3.1 General results	...82
3.3.2 Community structure	...82

3.3.3 Species dominance	...82
3.3.4 Phenology	...83
3.3.5 Species level phenology	...83
3.3.6 Environmental variables and lag effects	...84
3.3.7 Environmental variables and lag effects-species level	...84
3.4 Discussion	...85
3.4.1 Community structure	...86
3.4.2 Phenology	...86
3.4.3 Species level dominance and phenology	...86
3.4.4 Environmental variables and lag effects	...87
3.4.5 Environmental variables and lag effects-species level	...88
3.4.6 Conclusions	...89
3.5 References	...90
3.6 Tables and Figures	...97
3.7 Connecting Statement	...101
Thesis summary and conclusion	...102

Abstract

Globally, mosquitoes represent one of the most medically and economically important group of arthropods. Despite this, the ecology and distribution of mosquitoes is poorly understood in many parts of the world. The goal of this study was to examine mosquito population ecology and community structure across a variety of habitat types on the West Island of Montreal (Quebec, Canada) over a two year period (2014 & 2015). Mosquitoes were collected from 20 fixed sampling locations spanning suburban backyards, fields and forests with the use of LED EVS traps baited with CO₂.

Chapter 1 is a literature review examining work conducted locally and across North America and explores how habitat and climatic conditions shape species distributions and community structure. Chapter 2 examines spatial patterns of community structure as this relates to three broad periurban habitats. Chapter 3 analyses temporal aspects including; inter-annual community structure, phenology, and the effect of temperature and precipitation using a lag effect model.

Our results demonstrate that different habitats produce distinct communities but these vary between years. Habitats with structural similarities have similar community structure. Forest and field habitat generate greater species diversity and abundance compared to suburban habitat. Species dominance is attributed to a few species that show consistency in habitat preference and timing of emergence. Timing of peak emergence and number of peaks for total mosquito abundance is variable between years. Temperature and precipitation may explain some of the observed patterns. These variables reveal biologically plausible patterns of association with mosquito abundance. Temperature seems to correlate with flight activity in the short term and precipitation may correlate with reproduction over longer periods.

Detailed ecological studies of mosquito community structure can provide important baselines that can help to streamline surveillance and management programmes. Understanding the environmental drivers of mosquitoes allows for a better awareness of the nuisance potential and risk of mosquito-borne disease transmission, within Quebec and beyond.

Résumé

Les moustiques représentent le groupes d'arthropodes ayant le plus d'impact médical et économique globalement. Cependant, l'écologie et la distribution des moustiques ne sont pas bien compris dans plusieurs parties du monde. Le but de ce projet de recherche est d'examiner la structure des communautés de moustiques à travers une multitude d'habitats dans l'ouest de l'île de Montréal (Québec, Canada) sur une période de deux ans (2014-2015). Les moustiques furent collectés dans 20 sites d'échantillonnage décrit comme étant soit des milieux périurbain, des champs ou des milieux forestiers en utilisant des pièges 'LED EVS' enrichi de CO₂.

Le chapitre 1 est une revue de la littérature traitant sur les travaux fait localement et en Amérique du Nord et s'intéresse à l'effet des conditions climatiques et de l'habitat sur la distribution et la structure des communautés. Le chapitre 2 examine le profil spatial de la structure des communautés en lien avec trois habitats périurbains distincts. Le chapitre 3 analyse l'aspect temporel de ce système en incluant la structure interannuel des communautés et la phénologie ainsi que l'effet de la température et des précipitations avec l'aide d'un modèle de décalage temporel.

Nos résultats démontrent que les différents habitats engendrent des communautés distinctes, mais que celles-ci peuvent varier annuellement. Quand nous examinons les similarités structurelles des habitats (e. g. deux types de forêts), les communautés sont similaires. Les habitats décrits comme champs ou forêts ont une plus grande diversité d'espèces et une abondance plus élevée comparés aux habitats périurbains. Seules certaines espèces sont dominantes et démontrent une préférence pour certains habitats et sont consistants dans leur période d'émergence. Les périodes de haute émergence variaient dépendant de l'année ainsi que le nombre de ces événements. La température et les précipitations peuvent en partie expliquer ces observations. Ces variables révèlent certains des mécanismes biologiques potentiels en lien avec l'abondance des moustiques. La température semble corrélée avec le niveau d'activité à court-terme et les précipitations agissent plutôt sur la reproduction, et ce, à plus long-terme.

Les études écologiques sur les communautés de moustiques nous fournissent des données de base sur les conditions environnementales affectant la composition des

communautés à travers le temps et l'espace. Ces données peuvent aider à l'amélioration des programmes de surveillance et de gestion des moustiques. Une meilleure compréhension de ces conditions environnementales permet une sensibilisation accrue à la nuisance et aux risques potentiels de la transmission de maladie par les moustiques.

List of Tables

Table 2.1. Total numbers of mosquito species collected in 2014 and 2015 from Montreal, Québec, Canada. (pg. 70)

Table 2.2. PERMANOVA post-hoc analysis habitat comparisons for 2014 & 2015. Significant P-values in boldface. (pg. 71)

Table 2.3. ANOVA results for abundance and richness across all sites for both 2014 & 2015. Significant P-values in boldface. (pg. 71)

Table 3.1. PERMANOVA results for the interactions of year and habitat for 2014 & 2015. P-values in bold are adjusted P-values following Post Hoc analysis. *= significant P-values. (pg. 97)

Table 3.2. Linear model fit for mosquito abundance against mean weekly temperature, total weekly precipitation, and MW temperature + TW precipitation for 2014 & 2015. Highest R^2 values appear in shaded boxes. Significant values indicated by (*). (pg. 97)

Table 3.3. Results from linear model fitting exploring the effect of environmental variables on abundance of four focal species using mean weekly temperature, total weekly precipitation and their combined effect across a 4-week lag period. Values in boldface represent the highest R^2 values for each species and (*) indicates a significant P-value ($P < 0.05$). (pg. 97)

List of Figures

Figure 2.1. Map of the study area located on the western tip of the island of Montréal, Canada. Insert shows sampling locations as black dots. Abbreviations: suburban locations (BDU=Baie d'Urfé, SADB=Sainte-Anne-de-Bellevue) Forested (SM=Sugar Maple, BRM=Beech-Red Maple, HEM=Eastern Hemlock) and Field. (pg. 72)

Figure 2.2. NMDS ordinations for both 2014 (top) and 2015 (bottom). Ellipses represent the SE about the mean for each site. Stress values: 2014 (0.070), 2015 (0.039). (pg. 73)

Figure 2.3. Mean number of individuals collected per trap for all six sites in 2014 (left) & 2015 (right). Boxes show the upper and lower quartiles, the horizontal line within the box shows the median value and the whiskers show the maximum and minimum observed values. (pg. 73)

Figure 2.4. Species richness for all six sites in both 2014 (Left) & 2015 (Right). Boxes show the upper and lower quartiles, the horizontal line within the box shows the median value and the whiskers show the maximum and minimum observed values. (pg. 74)

Figure 2.5. Total abundance, species richness and shared species for each habitat type for 2014 & 2015. Total number of mosquitoes collected appears first, numbers in bold indicate total number of species collected and numbers in parentheses show the number of unique species. Numbers in overlapping areas indicate the number of shared species. Total species collected (bold and underlined) as well as the total number of shared species for each year appear in the centre of each diagram. (pg. 74)

Figure 2.6. Stacked bargraphs depicting relative abundance of the five most abundant species collected from each of the six sites in both 2014 (left) and 2015 (right) Note: Four of these species were ranked highest in both years and the fifth position was held by different species in 2014 & 2015, these being *Aedes stimulans* and *Aedes provocans*, respectively. *Culex pipiens* is included due to WNV vector potential. (pg. 75)

Appendix 2.1. Appendix 1 Rarefied species richness for 2014, 2015 and truncated 2015 data sets (pg. 75)

Figure 3.1. Map of the study area showing trap locations and location of the Sainte-Anne-de-Bellevue Meteorological station located on the Western tip of the island of Montreal, Quebec, Canada. Suburban sites: Baie d'Urfé (BDU) and Sainte-Anne-de-Bellevue (SADB); Forest sites: Sugar Maple (SM), Beech-Red Maple (BRM) and Eastern Hemlock (HEM); Field sites (FIELD). (pg. 98)

Figure 3.2. NMDS ordination showing comparison on mosquito community structure across both sampling seasons (Stress: 0.0987). Four letter acronyms represent individual species (ex. AEVE = *Aedes vexans*). (pg. 98)

Figure 3.3. Seasonal community structure as shown by relative dominance of the four focal species compared to all other species collected in both 2014 (a) and 2015 (b). (pg. 99)

Figure 3.4. Weekly mosquito abundance, total weekly precipitation, and mean weekly temperature for 2014 (a) and 2015 (b). (pg. 99)

Figure 3.5. Patterns of species abundance based on proportion of maximum abundance for our four focal species in 2014 (left) and 2015 (right). Environmental parameters, temperature and precipitation beginning in week 14 and terminating with the end of the sampling season can be seen below. (pg. 100)

Format

This thesis is presented in manuscript style and is organized into a series of chapters. Chapter 2 will be submitted to *The Journal of Vector Ecology* and chapter 3 will be submitted to *Environmental Entomology*. Chapter 1 is a literature review which provides background information surrounding the topics introduced in the following two chapters and also acts to introduce the thesis rationale as well as the specific research questions and objectives.

Acknowledgements

First and foremost, I would like to thank my supervisors, Dr. Jim Fyles and Dr. Chris Buddle of the Department of Natural Resource Sciences of McGill University. Their support, guidance, provision of resources, and feedback on all aspects of this endeavour are what really helped make it possible. Thank you also to committee member, Dr. David Lewis who provided some valuable guidance early on in this process. Special thanks to those who allowed me access to private property in order to collect samples and for providing site location information. I would like to thank the tremendous efforts of all of those who accompanied me to the field for sample collection, in particular Pedro Grillo, Scott Pemberton and Marianna Dimauro. A huge thank you to my father who accompanied me nearly every single week for trap set up and sample collection. I would like to recognize the financial and logistic contributions from the Morgan Arboretum which are greatly appreciated. The Insect Ecology lab (Shaun Turney, Elyssa Cameron, Gail Macinnis, Jessica Turgeon, Anne-Sophie Caron) who helped with more than just contributions, which were many, including sample collection, editing and statistical knowhow, but also with providing a wonderful workspace and continued motivation and support, thank you. Financial support was generously provided by the F. Grey Woods Fellowship, the E. Melville DuPorte Award, the Molson Nature Reserve Award, the Graduate Student Award, and the National Science and Engineering Council of Canada (NSERC), in the form of a Discovery Grant to Chris Buddle. Last but not least, I would like to thank my family and friends for their support, but most of all, thank you to my wife and daughter who were my source of inspiration and who were there with me every step of the way.

Contribution of Authors

I collected and analysed all of the data and also wrote the literature review and manuscripts contained in this thesis. Both supervisors, Jim Fyles and Chris Buddle appear as co-authors on chapters 2 and 3 due to their large contributions to conceptual design, continued feedback and editing of these manuscripts. Details of the contributions of many others can be seen in the acknowledgements section above.

Chapter 1: Introduction and Literature Review

1.1 Introduction

1.1.1 Thesis Rationale

This thesis examines the abundance and diversity of mosquito populations and communities in habitats on the island of Montreal (Quebec, Canada). This region of Canada is characterized by a mix of large urban centres with adjacent suburban municipalities as well as an abundance of parks, forested areas, wetlands, fluvial waterbodies and agricultural land (Quebec Energy and Natural Resources, 2003; Environment and Climate Change Canada, 2015). The close proximity of these different habitats over a relatively small geographic area facilitates the movement of mosquitoes between habitats. This can subsequently increase the risk of periodic nuisance events or disease transmission to a large human population. By examining how habitat and environmental conditions shape mosquito abundance and diversity at the population and community levels, we will begin to better understand how these factors shape mosquito ecology in this region.

1.1.2 Research Objectives

The broad objective of this thesis is to determine how the abundance and diversity of mosquito populations and communities are shaped by habitat and environmental variables on the West Island of Montreal. The three habitat types considered here are suburban areas, fields, and forests, common habitat types in Southern Quebec. This will contribute invaluable knowledge to the distribution, phenology and ecology of important nuisance and potential vector species occurring within the region. These objectives will be met through two data chapters. Chapter 2 focuses specifically on the role of habitat in shaping populations and communities. It also focuses on the abundance, diversity and interaction of species occurring within, and between these habitats. Chapter 3 is focused on the temporal changes to populations and communities within these same habitats, comparing communities and phenology seasonally, and across multiple sampling years. This chapter also investigates the relationship between mosquito abundance and the environmental variables; temperature and precipitation. Chapter 1 establishes the context of this

research, from the historical and current research occurring in North America, to the interactions between mosquitoes and their environment, to the techniques and considerations for sampling and modeling.

The specific objectives of this thesis are therefore summarised as follows:

Chapter 1

The objective of this chapter is to review the literature and provide background information on mosquito research in the context of North America. It will examine the interactions between mosquitoes and environmental conditions, specifically habitat and environmental (meteorological) variables. It will also provide an overview of mosquito sampling, identification and monitoring techniques.

Chapter 2

The primary objective of this chapter is to determine how habitat plays a role in shaping mosquito communities in three dominant habitat types (suburban, field, and forest) found in this region. A second objective is to address specific patterns of abundance, species richness and species sharing across all habitats and to identify patterns of relative abundance in the dominant species found across all habitats.

Chapter 3

One objective of this chapter is to quantify the temporal variation in mosquito community structure through analysis of community composition and relative dominance across all habitats over two years. A second objective is to describe the patterns of annual phenology at the level of community and that of dominant species. Finally, this chapter will examine the relationship between temperature and rainfall and how this influences mosquito abundance at weekly lag intervals.

1.2 Mosquito research in North America

With nearly 3,600 species worldwide (Wilkerson et al., 2015), the mosquitoes (Diptera: Culicidae) are among the most medically and economically important insects on Earth. Although mosquitoes are known mostly for their negative impacts (e.g., as vectors for globally important diseases such as malaria (Guinovart et al., 2006; Gubler, 2010)), the majority of species do not bite people or livestock and some have important ecological roles as pollinators (Singer, 2001; Döetterl et al., 2012) or as important food sources for other organisms (Rueda, 2008; Gonsalves et al., 2013). Interest in studying mosquitoes dates back over a century and stemmed from their potential as serious nuisance pests as well as their role in the transmission of disease to both humans and livestock (Becker et al., 2003; Silver, 2008; Williams, 2010; Halasa et al., 2014). A look at modern literature reveals an abundance of work related to mosquito importance as vectors of various pathogens and how they are closely linked to human habitats. Much of this research focuses on a particular species, or on the specific pathogens they transmit.

In North America, a great deal of research has been done since the early 1900s to better understand the biology of mosquitoes. This was sparked by the discovery of the association between mosquitoes and life threatening pathogens like malaria and yellow fever (Matheson, 1929). Some of the earliest works in trying to map and describe the natural history of mosquitoes of North America dates back to 1912-1917 by Howard, Dyar and Knab in “The Mosquitoes of North and Central America and the West Indies” (1917). Since then, several large works have focused solely on the mosquito fauna of North America. These works were aimed primarily at identifying the range of known species, while others focused on a combination of life history and phenology as well as taxonomy and distribution. Each installment of literature since these early beginnings has seen sometimes dramatic changes from one to the next. A good example is in the number and range of species of the continent. Dyar (1928) compiled his “The Mosquitoes of North America” where he claims a total of 123 species for the continent and suggests that not many more would be found. Shortly thereafter, Bates (1949) declared similar numbers with 121 species. Over the next 60 years, the number of mosquito species known in North America has climbed ever higher. Carpenter and

Lacasse (1955) compiled one of the first comprehensive manuals on mosquitoes of North America in which they described 143 species. By the 1980's, that number had climbed to 167 (Darsie & Ward, 1981) and in a more recent publication, a total of 174 species was described (Darsie & Ward, 2005).

Within the Canadian context, the reported number of mosquito species has climbed from 74 in the 1970's (Wood et al., 1979) to 79 in the 80's (Darsie & Ward, 1981) to 80 (Darsie & Ward, 2005) and now, most recently 82 species (Thielman & Hunter, 2007). Aside from taxonomic revisions and resolution (Reinert, 2000; Cywinska et al., 2006; Wilkerson et al., 2015), the accidental introduction of alien species via international trade and travel (Benedict et al., 2007; Bonizzoni et al., 2013; Kampen & Werner, 2014), or the northward expansion of more southern species, likely due to climate warming which can explain some of the changes in species distribution (Yee, 2008; Hongoh et al., 2012; Rochlin et al., 2013). These changes to distribution coupled with an ever-changing climate are a good indication that mosquito fauna should be studied continually to track changes in phenology (temporal bionomics) and species occurrence patterns. This knowledge can help predict outbreaks, assess the risk of disease transmission and improve on management strategies, as many of the species in Canada are known human biters (Wood et al., 1979) and many are capable of transmitting disease (CDC, 2012).

Mosquito research within the province of Quebec has been ongoing for many years. Much of the focus has been given to mapping the distribution of mosquitoes in association to different habitats. Many of these studies examined larval or adult mosquito communities associated with common wetland types, such as string bogs (Maire, 1982) or cattail marshes (Leprince & Lewis, 1982). Most of the locations sampled were somewhat remote and not very close to large urban centres of which the province has several. In 1998 a survey of vernal pools was conducted at the Morgan Arboretum, a forested reserve located just minutes from Montreal, the largest urban centre in Quebec (Doran & Lewis, 2003). This study revealed that many species of mosquitoes can be found in proximity to

urban centres and reveals patterns of community composition, relative abundance and seasonal phenology.

Much of the recent focus is on the surveillance of arthropod-borne viral (Arbovirus) infections. The only mosquito-borne infection which is currently under surveillance in Quebec is the West Nile Virus (WNV) (MSSS, 2016) although others such as Eastern Equine Encephalitis are also known (Rocheleau et al., 2013). In Eastern Canada, the most common vectors of WNV are mosquitoes in the genus *Culex*, in particular, *Cx. pipiens* (Andreadis et al., 2001; Turell et al., 2005). Aside from being vectors of disease, many species occurring in Canada can be an appreciable nuisance as they feed aggressively on humans throughout most of the summer months (Wood et al., 1979). Since the discovery of WNV in North America in 1999, many routine sampling surveys and surveillance programs have been established which attempt to track not only West Nile Virus but mosquito populations as a whole (Marfin et al., 2001; Thielman & Hunter, 2006; Giberson et al., 2007; McMahon et al., 2008).

The first cases of WNV appeared in Quebec in 2002 and since then, intensive monitoring strategies have been put in place to monitor its progression (Gosselin et al., 2005; El Adlouni et al., 2007). Province-wide mosquito surveillance and collection of infection data is handled by the Ministère de la Santé et des Services sociaux (MSSS). For as long as the disease has been known in the province, it has been mandatory for healthcare providers and laboratory workers to report all WNV cases to public health authorities (MSSS, 2016). These reports allow for better tracking of potential hotspots and seasonality of the virus as well as the vectors and zoonotic reservoirs (birds) involved with transmission. Through monitoring, patterns of occurrence have begun to emerge which link mosquitoes to a variety of habitats. Findings show *Culex* spp. and others like the invasive and WNV competent “Asian bush” or “Asian rock pool” mosquito (*Aedes japonicus japonicus*) (Theobald) are species closely tied to human dwellings and reproduce effectively in waste containers (Thielman and Hunter, 2006; Kaufman & Fonseca, 2014). One of the more recent studies based on habitat mapping in Montreal was conducted by Pritchard (2010). The study analysed the blood meal sources collected

in wild female mosquitoes and also linked this to habitat type. This revealed the distribution of prominent blood hosts used by mosquitoes across rural, suburban and urban environments. Findings from these surveillance programs highlight a need to better understand where mosquitoes can be found with respect to available habitats and also the drivers of population fluctuations.

Despite the volume of work done to identify the range and biology of mosquito species in North America (Barker et al., 2003; Juliano & Lounibos, 2005; Pecoraro et al., 2007; Haddow et al., 2009; Andreadis & Wolfe, 2010; Buckner et al., 2011; Ganser & Wisely, 2013), the precise distribution and habitat preferences of most species is still unknown. Annual variations within communities and fluctuations in phenology seem to be species-specific and from one year to the next these changes can be pronounced, making predictions about mosquito abundance difficult (Schäfer et al., 2008; Godsey et al., 2010; Lysyk, 2010; Deichmeister & Telang, 2011). Improving our knowledge of mosquito populations requires that we study their ecology in detail (Alencar et al. 2015).

1.3 Effect of habitat on mosquito communities

As with all organisms, mosquito distribution is a function of the suitability of a habitat to support their basic biological requirements. Habitat is often considered a major driver in shaping local mosquito communities. The suitability of a given habitat depends largely on the physical structure, such as the availability of breeding sites, but also on environmental conditions, species interactions and the number of potential hosts (Andreadis & Wolfe, 2010; Buckner et al., 2011; Yi et al., 2014; Golding et al., 2015). Arthropods respond to the structural complexity of a habitat (Zhong et al., 2003; Maleque et al., 2006). Structural complexity in the case of a forest, for instance, refers to things like overstory composition, stand age, vertical strata and the composition of the forest floor (Maleque et al., 2006). All habitats, whether urban areas, agricultural land, or pristine wild areas, contain structure or habitat elements which can provide some essential resources for survival. Human-altered habitats can sometimes increase the likelihood of mosquito related problems due to the expansion or creation of ideal

habitat conditions, sometimes resulting in increased mosquito populations (Norris, 2004).

Mosquito communities are not distributed equally, temporally or spatially, in a given landscape, due in part to environmental differences, habitat variability, ability to disperse, and host-seeking behavior (Zhong et al., 2003). Since mosquitoes rely on their habitat for resting, feeding and reproduction, these elements are important in assessing the relationship they have with a given habitat. Scale is an important consideration when associating habitat structures to mosquito presence and abundance. Landscape connectivity and the distribution of different habitat types appears to have an effect on how mosquito communities are distributed (Diekötter & Crist, 2013; Abella-Medrano et al., 2015). Burkett-Cadena et al. (2008) evaluated these small habitat elements and determined that most species examined exhibited significant preference for resting on a given substrate type (leaves vs. artificial structures, e.g., garbage cans) during adverse weather or periods of inactivity. Their findings revealed little variability in these preferences. Early studies of long range visual orientation by mosquitoes demonstrated that although most have habitat preferences for resting as adults, many will wander to different areas in response to stimuli like traps or hosts (Bidle & Hem, 1981). When looking at large scale preferences in habitat, Schäfer et al. (2006) noted that most mosquito species had highest abundance when associated with large scale forested areas with abundant temporary water sources vs. open areas with more permanent water.

Different studies of patterns in diversity related to habitat structure have found conflicting results. Zhong et al. (2003) found an increase in species richness with increasing habitat complexity. These habitats offer a variety of landscape features with increased structure. Similarly, Stein et al. (2016) found that semi-urban and pristine wild areas contained the greatest richness of species compared to more human altered environments. In contrast, Abella-Medrano et al. (2015) found that diversity was highest in sites located closer to urban areas with higher disturbance. Species level variability with respect to habitat structure is to be expected, but Junglen et al. (2009) also noted

significant variability with respect to habitat preference at the genus level within forests of different age classes and within proximity to disturbed human settlements. Arguably one of the most important elements offered by a particular habitat is the availability of breeding sites and this likely results in differences observed in the composition of local mosquito fauna (Yan & Zhong, 2005; Alencar et al., 2015). Many mosquito species preferentially select ephemeral biotopes for reproduction as these favor accelerated population increase (Clements, 1992). These breeding sites vary in size, longevity, frequency and faunal composition depending on their availability and location within a habitat (Schneider & Frost, 1996). Breeding sites in general range in origin from permanent water to vernal pools, generally maintained following snowmelt (Williams et al., 2010), to plant-based reservoirs such as those found in bromeliads (Frank & Lounibos, 2009), tree holes (Ellis et al., 2006) and the leaves of some carnivorous plants (Armbruster et al., 1997). Man-made containers ideally suited to retaining water, such as discarded tires, bird baths and clogged gutters are also widely used, particularly in more human-altered environments (Richards et al., 2008; Rueda, 2008; Yee et al., 2010). Despite classification as one breeding type (ex. ground-water, artificial-container, phytotelm, etc.), the ability to withstand starvation and variability in development time allows certain species to survive in just about any habitat regardless of the breeding site type or quality (Barrera & Medialde, 1996).

Other factors that determine where mosquitoes can be found are the ability of individual species to locate resources, and their ability to disperse from source areas (Schowalter, 2011). Wind dispersal is a way that mosquitoes can locate hosts or breeding sites and it has been shown that short, medium or long range wind dispersal can be common with mosquitoes (Service, 1980; Cummins et al., 2012), thus increasing habitat utilization potential. Not all species disperse far from breeding sites, making them more specialist in a given habitat. This is known particularly for those species breeding in proximity to human settlements (Bellini et al., 2010; Hamer et al., 2014). Despite a wealth of information pertaining to habitat preference and local ranges, much of what we know about the current distribution of species in Canada is based on extrapolation of strongly verified, yet irregular and relatively few accounts or records (Darsie & Ward, 2005).

Thus, research focusing on the habitat drivers of abundance and community structure are important for understanding the fluctuations both seasonally and annually for any given location.

1.4 Effect of environmental variables on mosquito communities

Insects respond strongly to environmental conditions. In temperate seasonal regions, a multitude of environmental or climatic variables play a role in shaping insect behavior, development, abundance, seasonality, and dispersal (Kingsolver, 1989; Speight et al., 1999). For mosquitoes, these factors include, but are not limited to; snow depth and winter temperature (El Adlouni et al., 2007; Andreadis & Wolfe, 2010; Hongoh et al., 2012; Rochlin et al., 2013), springtime temperature (Lysyk, 2010; Ciota et al., 2014) seasonal rainfall events (Wood et al., 1979; Crans, 2004; Godsey et al., 2010), wind speed and direction (Service, 1980), photoperiod (Guedes & Navarro-Silva, 2014; Roiz et al., 2014) and the seasonal abundance of host species (Kilpatrick et al., 2006; Chaves et al., 2010). Late summer drop off, diapause induction, and overwinter survival are also related to many of these factors, but primarily colder temperatures, reduced rainfall and photoperiod (Tauthong & Brust, 1977; Lysyk, 2010, Roiz et al., 2014). Overwinter survival strategies of mosquitoes are discussed in detail by Crans (2004).

Mosquitoes in Canada exhibit several generalized overwintering types. Mosquito populations show variation in date of peak abundance from year to year (Godsey et al., 2010). The variability in seasonality and abundance from one year to another can sometimes be explained by stochastic weather such as a single large rainfall event (Godsey et al., 2010) or by the temperature array within a given year (Deichmeister & Telang, 2011). The influence of climate on mosquitoes is scale and species dependent (Roiz et al., 2014). The interplay of environmental variables is complex and many simultaneous variables are at work. Thus, results from one study of the effects of climate on mosquito populations cannot be extrapolated between climate regions, reinforcing the need for multiple studies (Ewing et al., 2016).

Many studies have identified temperature as a main driver of abundance and activity of mosquitoes and noted significant positive relationships between these factors (DeGroot et al., 2007; Pecoraro et al., 2007; Lysyk, 2010; Deichmeister & Telang, 2011; Ganser & Wisely, 2013; Jacups et al., 2015). Mosquitoes respond to temperature within a particular range, and this itself is species-specific (Clements, 1992; Buckner et al., 2011; Roiz et al., 2014). Cold temperatures can slow development, reduce flight activity and feeding, and induce diapause (Clements, 1992; Crans, 2004; Clements, 2013). Warm temperatures, however, tend to speed up development by increasing metabolism resulting in shorter generation time of larvae or pupae (Doran & Lewis, 2003; Paaajmans et al., 2010), decrease the time between blood meals (Ruiz et al., 2010; Ciota et al., 2014; Shand et al., 2016) and increase adult longevity and feeding frequency (Becker, 2008; Ciota et al., 2014). High temperatures also exhibit a maximum threshold and above that, adult longevity begins to decrease (Roiz et al., 2014). Many studies on the effect of temperature often consider not only the response of mosquitoes, but also of associated pathogens. Like their insect hosts, pathogenic organisms can respond to temperature through decreased incubation time, increased replication, and faster dissemination and transmission (Martens et al., 1997; Kilpatrick et al., 2008) up to maximal levels.

Precipitation is commonly considered one of the primary drivers of mosquito abundance. Because mosquitoes use aquatic habitats for reproduction and many of these result from precipitation events, rainfall in particular is often regarded as a limiting factor in the availability of breeding sites affecting larval success which later translates into adult mosquito abundance (Shaman & Day, 2007; Gong et al., 2011). High frequency and intensity of rainfall events can result in larger populations of mosquitoes and also influence the number of generations in a given year which are important variables in nuisance and vector cycles (Horsfall et al., 1973; Bicout & Sabatier, 2004; Hu et al., 2006; Ponçon et al., 2007). Jacups et al. (2015) found that rainfall events occurring up to two weeks before mosquito collection had a significant effect on when certain species peaked, suggesting a strong association between these two variables. Similarly, Ruiz et al. (2010) noticed an increase in mosquito infection rates with WNV 1-

3 weeks after a rainfall event. Shaman & Day (2007) noted that mosquito populations can increase rapidly in response to moderate to heavy rainfall events if appropriately timed to natural reproductive rhythms. These rainfall events were an important consideration in the transmission of disease, and they noted also that the secondary effects of precipitation, namely, near-surface humidity, also triggered a response. Ruiz et al. (2010) also noted possible association with surface humidity and soil moisture, stating that these variables likely play subtle roles in mosquito success and can explain some of the patterns they observed, but not nearly as clearly as patterns observed with temperature.

Precipitation can also produce negative effects on mosquito populations. The idea of “flushing” of larvae from breeding sites has been observed by several authors (Paaijmans et al., 2007; Koenraadt & Harrington, 2008; Deichmeister & Telang, 2011). Even when faced with drought conditions, some mosquito populations respond positively, a finding counterintuitive to the association between mosquitoes and aquatic environments. Reasons for this include reductions in competition or predation pressure from other species which require more permanence in water bodies (Chase & Knight, 2003). Increases in human water harvesting behavior also increase when faced with drought, resulting in suitable habitat formation (Trewin et al., 2013). Although results from past studies do represent biologically plausible findings with respect to mosquito fauna in response to precipitation, it has been determined that, in general, temperature is a better predictor when considering environmental variables as drivers of abundance (Pecoraro et al., 2007; Becker, 2008).

Despite knowledge on thresholds and responses to environmental variables and how this translates into mosquito bionomics, we still do not have a firm understanding of how these variables affect mosquitoes or the pathogens they may transmit (Gong et al., 2011). Understanding how these environmental variables influence mosquito population dynamics is critical to our understanding of their nuisance potential and medical importance.

1.5 Sampling mosquitoes

Trapping of mosquitoes and assessing abundance and species composition are integral in the establishment of surveillance programs and management strategies. As with any insect sampling, the life stage that is sampled and the collection method present inherent bias (Brown et al., 2008). Sampling of larvae is usually accomplished through dipping in selected habitats (Hagstrum, 1971; Rydzanicz & Lonc, 2003; Shililu et al., 2003), yet does not allow for assessment of the adult mosquito population or biting activity. Many factors must be considered when setting up a sampling protocol for adult mosquitoes, e.g., trap type, trap placement, habitat selection, time of day, season, attractants used, etc. (Williams et al., 2007; Brown et al., 2008). Light traps are commonly used in surveillance programs and population studies because they often yield large numbers of mosquitoes of a variety of species (Silver, 2008). Light trap efficiency has been debated many times and comparative studies on trap types and baits have been performed (Ritchie & Klein, 1995; Cohnstaedt et al., 2008; Silver, 2008; Bisevac et al., 2009; Govella et al., 2011). Baited light traps which use dry ice (CO₂) most often collect unfed females in search of a blood-meal. This allows the data collected to be interpreted more in terms of biting (nuisance or vector) potential (Davis et al., 1995; Silver, 2008; Chuang et al., 2011) compared to larval sampling. Typically used to capture species of significant medical importance (ex. *Culex pipiens*) as part of vector studies, they can also be used to detect fluctuations in abundance, seasonality and dispersal of a multitude of species. Mosquito dispersal patterns have also been assessed by using techniques involving stable isotopes in combination with light traps. These inert compounds are used to mark mosquito larvae from either man-made or naturally occurring waterbodies and upon collection of blood-seeking adults, population dispersal patterns have been assessed (Hamer et al., 2012; Hamer et al., 2014; Opiyo et al., 2016). There are drawbacks to using light traps, however, as some species can be repelled by light sources, and when dry ice is added, the cold air generated around traps can deter certain species (Zhong et al., 2003; Silver, 2008). Because of this, it has been suggested that, to best represent the abundance and diversity of mosquitoes in a given area, light traps should be accompanied by larval sampling (Collett et al., 1964), although, combining methods could be time consuming and labor intensive.

Other trap types used for the study of adult female mosquitoes include resting boxes and gravid traps. Adult mosquitoes spend a lot of time resting and not actively searching for blood meals (Silver, 2008). By using resting boxes to provide mosquitoes with a secure location to rest, adult females both unfed and previously blood fed, as well as males can be collected. Gravid traps are used to sample females that have already collected a blood meal and are searching for oviposition sites. By using a plant based infusion in water, artificial breeding sites are created which are highly attractive to mosquitoes (Lee & Kokas, 2004). When using gravid traps, Williams & Gingrich (2007) detected infection rates of adult females with WNV was nearly 33 times higher than that of standard light traps. They suggest that with respect to arbovirus surveillance, gravid traps are superior. It is generally agreed that any adult mosquito collection programs should take place at the very start of the flight season and extend until the very end. In temperate regions, this is from spring, shortly after snowmelt, to the end of the fall (Marfin et al., 2001). Samples collected at weekly intervals appear to be the standard with respect to ecological monitoring or vector surveillance as seen by the abundance of studies performed (Ryan et al., 2004; Ginsberg et al., 2010; Godsey et al., 2010; van den Hurk et al., 2012; Pepin et al., 2013). These long term data can provide a clearer picture of seasonal and annual phenology and peak activity times. Despite the variety of trap types and the large number of current surveillance programs in place, Zhong et al. (2003) observed that much of the data collected for these studies do not get used for ecological interpretation. By analysing data related to distributions across habitats and seasonal abundance for a diversity of species, more ecologically based population trends can be generated, contributing knowledge about the habitat utilization and phenology of these nuisance pests or vectors of disease.

1.6 Modeling mosquito populations

Predictive modeling is now commonplace in the field of mosquito ecology. Modeling allows for a degree of predictive power with respect to mosquito population fluctuations, range expansion and disease outbreaks. Many modeling studies rely mosquito collection data or information pertaining to incidence of disease. This is often used in combination with environmental parameters such as landscape or climactic variables

taken from historical records or collected via data loggers to generate patterns (Ruiz et al., 2010; Gong et al., 2011; Roiz et al., 2014; Shand et al., 2016). Weather patterns will greatly influence mosquitoes and thus appear frequently as explanatory variables in models. Often, time lag effects are tested against observed mosquito abundance or infection data. This allows for better detection of the biological relationships that mosquitoes exhibit to these environmental variables (Roiz et al., 2014; Jacups et al., 2015). Similarly, many models use current knowledge of global climate change as a model of future climatic conditions and extrapolate mosquito response based on this (Patz et al., 1998; Patz et al., 2005; Roiz et al., 2014). However, Buckner et al. (2011) noticed that the predictive power of variables such as temperature, precipitation and humidity are generally species specific thus making generalization difficult. Another hurdle in the adoption of effective generalized models is that many difficult to quantify variables exist, examples being socio-economic development, current mosquito abatement practices or land use alterations in a given location (Ruiz et al., 2010; Kilpatrick, 2011; Roiz et al., 2014; Jacups et al., 2015). Site specific environmental conditions, and the interaction of these conditions, limit the ability to simulate abundance at the scale of microclimate, yet also limit our ability to extrapolate these into large scale patterns (Gong et al., 2011; Ewing et al., 2016). Temperature gleaned from weather stations may not accurately depict temperatures experienced in urban and suburban areas due to slight microclimate differences. Cator et al. (2013) noted differences of 1-3°C and found that these differences, as well as the reduction in temperature fluctuations experienced between day and night, can interfere with the ability to predict the effect of temperature on mosquito life cycles, especially in developed habitats. Models should then be place-specific, as spatial scales become very important pieces to the modeling puzzle.

Rochlin et al. (2013) used statistical modeling to map the current and possible future distribution of an invasive mosquito species (*Aedes albopictus*) (Skuse), incorporating presence data gleaned from a local surveillance database and environmental variables from global climate databases. These analysis tools can predict future range expansion by incorporating landscape and environmental variables from the present and compare

these to a set of altered environmental conditions under the predicted influence of climate change. This modelling predicts that, within a few decades, many new regions will become suitable for this species as a result of land use changes and global climate change. Their results point to the interplay of snow depth and winter temperatures as important considerations and that mean winter temperature is the main limiting factor to the species current distribution. El Adlouni et al. (2007) who, when examining the climatic conditions responsible for WNV outbreaks in several North American cities, found an important link between winter temperature thresholds from the previous year and summer temperature thresholds in the year of infection, suggesting the importance of a multi-year approach. These findings were directly responsible for reshaping the management approaches for larval mosquito control in the province of Quebec. A study that utilized between-year climatic data conducted by Ruiz et al. (2010) found that for virus infection rates in mosquitoes, a negative correlation exists with respect to precipitation in the previous year. Studies such as these, which utilize inter-annual data, are important for long term trend identification.

1.7 New technology for mosquito taxonomy and monitoring

Mosquitoes of some genera can be particularly difficult to identify correctly to species, but new technologies are being developed that may aid in this. DNA barcoding is certainly a tremendous advance with respect to species level identifications, and has proven effective with Canadian species (Cywinska et al., 2006). Other methods, such as identification using computer-automated systems are also being tested. These methods use two dimensional images of insect body parts, typically wings, to generate identifications based on wing venation patterns derived from reference specimens. Tests have shown that the accuracy of these techniques is comparable to the success achieved by taxonomists who specialize in a particular group, and so seem very promising as a method of identification (Favret & Sieracki, 2015). Schneider et al. (2016) recently conducted a study using environmental DNA (eDNA) as a method to detect the presence of invasive mosquito species. They sampled water bodies which were suitable for these species and tested the samples for DNA traces. Their results show that surveillance using eDNA was congruent with other available methods and

argue that this method is reliable and effective. Schneider et al. (2016) believe this technique has tremendous potential for wide-scale mapping of mosquito populations through citizen science contribution. The USDA has also begun engaging the public in programs that encourage citizens or school groups to submit samples to their labs for identification, allowing for a large scale snapshot of mosquito distribution (USDA, 2016). As technologies and efforts continually evolve, so will our understanding of mosquito ecology.

1.8 References

- Abella-Medrano, C. A., Ibáñez-Bernal, S., MacGregor-Fors, I., & Santiago-Alarcon, D. (2015). Spatiotemporal variation of mosquito diversity (Diptera: Culicidae) at places with different land-use types within a neotropical montane cloud forest matrix. *Parasites & Vectors*, 8(1), 1.
- Alencar, J., de Mello, C. F., Guimarães, A. É., Gil-Santana, H. R., dos Santos Silva, J., Santos-Mallet, J. R., & Gleiser, R. M. (2015). Culicidae community composition and temporal dynamics in Guapiaçu Ecological Reserve, Cachoeiras de Macacu, Rio de Janeiro, Brazil. *PloS ONE*, 10(3), e0122268.
- Andreadis, T. G., Anderson, J. F., & Vossbrinck, C. R. (2001). Mosquito surveillance for West Nile virus in Connecticut, 2000: isolation from *Culex pipiens*, *Cx. restuans*, *Cx. salinarius*, and *Culiseta melanura*. *Emerging Infectious Diseases*, 7(4), 670.
- Andreadis, T. G., & Wolfe, R. J. (2010). Evidence for reduction of native mosquitoes with increased expansion of invasive *Ochlerotatus japonicus japonicus* (Diptera: Culicidae) in the northeastern United States. *Journal of Medical Entomology*, 47(1), 43-52.
- Armbruster, P., Bradshaw, W. E., & Holzapfel, C. M. (1997). Evolution of the genetic architecture underlying fitness in the pitcher-plant mosquito, *Wyeomyia smithii*. *Evolution*, 51(2) 451-458.
- Barker, C. M., Paulson, S. L., Cantrell, S., & Davis, B. S. (2003). Habitat preferences and phenology of *Ochlerotatus triseriatus* and *Aedes albopictus* (Diptera: Culicidae) in southwestern Virginia. *Journal of Medical Entomology*, 40(4), 403-410.

- Barrera, R., & Medialdea, V. (1996). Development time and resistance to starvation of mosquito larvae. *Journal of Natural History*, 30(3), 447-458.
- Bates, M. The natural history of mosquitoes. 1949. The Macmillan Company. New York, NY. 379 pp.
- Becker, N., Petrić, D., Zgomba, M., Boase, C., Dahl, C. Lane, J., & Kaiser, A. (2003). Mosquitoes and their control. Springer. New York, NY. 577 pp.
- Becker, N. (2008). Influence of climate change on mosquito development and mosquito-borne diseases in Europe. *Parasitology Research*, 103(1), 19-28.
- Bellini, R., Albieri, A., Balestrino, F., Carrieri, M., Porretta, D., Urbanelli, S., Calvitti, M., Moretti, R., & Maini, S. (2010). Dispersal and survival of *Aedes albopictus* (Diptera: Culicidae) males in Italian urban areas and significance for sterile insect technique application. *Journal of Medical Entomology*, 47(6), 1082-1091.
- Benedict, M. Q., Levine, R. S., Hawley, W. A., & Lounibos, L. P. (2007). Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*. *Vector-borne and Zoonotic Diseases*, 7(1), 76-85.
- Bicout, D. J., & Sabatier, P. (2004). Mapping Rift Valley fever vectors and prevalence using rainfall variations. *Vector-borne and Zoonotic Diseases*, 4(1), 33-42.
- Bidlingmayer, W. L., & Hem, D. G. (1981). Mosquito flight paths in relation to the environment. Effect of the forest edge upon trap catches in the field. *Mosquito News*, 41(1), 55-59.
- Bisevac, L., Franklin, D. C., Williamson, G. J., & Whelan, P. I. (2009). A comparison of two generic trap types for monitoring mosquitoes through an annual cycle in tropical Australia. *Journal of the American Mosquito Control Association*, 25(1), 58-65.
- Bonizzoni, M., Gasperi, G., Chen, X., & James, A. A. (2013). The invasive mosquito species *Aedes albopictus*: current knowledge and future perspectives. *Trends in Parasitology*, 29(9), 460-468.
- Brown, H. E., Paladini, M., Cook, R. A., Kline, D., Barnard, D., & Fish, D. (2008). Effectiveness of mosquito traps in measuring species abundance and composition. *Journal of Medical Entomology*, 45(3), 517-521.

- Buckner, E. A., Blackmore, M. S., Golladay, S. W., & Covich, A. P. (2011). Weather and landscape factors associated with adult mosquito abundance in southwestern Georgia, USA. *Journal of Vector Ecology*, 36(2), 269-278.
- Burkett-Cadena, N. D., Eubanks, M. D., & Unnasch, T. R. (2008). Preference of female mosquitoes for natural and artificial resting sites. *Journal of the American Mosquito Control Association*, 24(2), 228.
- Carpenter, S. J., & LaCasse, W. J. (1955). *Mosquitoes of North America*. University of California Press. Berkeley, California. 360 pp.
- Cator, L. J., Thomas, S., Paaijmans, K. P., Ravishankaran, S., Justin, J. A., Mathai, M. T., Read, A. F., Thomas, M. B., & Eapen, A. (2013). Characterizing microclimate in urban malaria transmission settings: a case study from Chennai, India. *Malaria Journal*, 12(1), 1.
- CDC Centres for Disease Control. (2012). Mosquito species in which West Nile Virus has been detected, United States, 1999-2012. Accessed September 2014.
Retrieved from:
<http://www.cdc.gov/westnile/resources/pdfs/MosquitoSpecies1999-2012.pdf>
- Chase, J. M., & Knight, T. M. (2003). Drought-induced mosquito outbreaks in wetlands. *Ecology Letters*, 6(11), 1017-1024.
- Chaves, L. F., Harrington, L. C., Keogh, C. L., Nguyen, A. M., & Kitron, U. D. (2010). Blood feeding patterns of mosquitoes: random or structured? *Frontiers in Zoology*, 7(1), 1.
- Chuang, T. W., Hildreth, M. B., Vanroekel, D. L., & Wimberly, M. C. (2011). Weather and land cover influences on mosquito populations in Sioux Falls, South Dakota. *Journal of Medical Entomology*, 48(3), 669-679.
- Ciota, A. T., Matacchiero, A. C., Kilpatrick, A. M., & Kramer, L. D. (2014). The effect of temperature on life history traits of *Culex* mosquitoes. *Journal of Medical Entomology*, 51(1), 55-62.
- Clements A. N. (1992). *The Biology of Mosquitoes: Growth, nutrition and reproduction*. Chapman & Hall. London. 536 pp.
- Clements, A. N. (2013). *The physiology of mosquitoes: international series of monographs on pure and applied biology: zoology*. Science (17). Elsevier. 404 pp.

- Cohnstaedt, L. E. E., Gillen, J. I., & Munstermann, L. E. (2008). Light-emitting diode technology improves insect trapping. *Journal of the American Mosquito Control Association*, 24(2), 331.
- Collett, G. C., Graham, J. E., & Bradley, I. E. (1964). Relationship of mosquito light trap collection data to larval survey data in Salt Lake county. *Mosquito News*, 24(2), 160-162.
- Crans, W. J. (2004). A classification system for mosquito life cycles: life cycle types for mosquitoes of the northeastern United States. *Journal of Vector Ecology*, 29, 1-10.
- Cummins, B., Cortez, R., Foppa, I. M., Walbeck, J., & Hyman, J. M. (2012). A spatial model of mosquito host-seeking behavior. *PLoS Computational Biology*, 8(5), e1002500.
- Cywinska, A., Hunter, F. F., & Hebert, P. D. (2006). Identifying Canadian mosquito species through DNA barcodes. *Medical and Veterinary Entomology*, 20(4), 413-424.
- Darsie Jr, R. F., & Ward, R. A. (1981). Identification and geographical distribution of the mosquitoes of North America, north of Mexico. Walter Reed Army Institute of Research. Washington, D.C. 313 pp.
- Darsie Jr, R. F., & Ward, R. A. (2005). Identification and geographical distribution of the mosquitoes of North America, north of Mexico. *Journal of the American Mosquito Control Association*, 21(1), 383 pp.
- Davis, J. R., Hall, T., Chee, E. M., Majala, A., Minjas, J., & Shiff, C. J. (1995). Comparison of sampling anopheline mosquitoes by light-trap and human-bait collections indoors at Bagamoyo, Tanzania. *Medical and Veterinary Entomology*, 9(3), 249-255.
- DeGroote, J., Mercer, D. R., Fisher, J., & Sugumaran, R. (2007). Spatiotemporal investigation of adult mosquito (Diptera: Culicidae) populations in an eastern Iowa county, USA. *Journal of Medical Entomology*, 44(6), 1139-1150.
- Deichmeister, J. M., & Telang, A. (2011). Abundance of West Nile virus mosquito vectors in relation to climate and landscape variables. *Journal of Vector Ecology*, 36(1), 75-85.

- Diekötter, T., & Crist, T. O. (2013). Quantifying habitat-specific contributions to insect diversity in agricultural mosaic landscapes. *Insect Conservation and Diversity*, 6(5), 607-618.
- Döetler, S., Jahreib, K., Jhumur, U. S., & Juergens, A. (2012). Temporal variation of flower scent in *Silene otites* (Caryophyllaceae): a species with a mixed pollination system. *Botanical Journal of the Linnean Society*, 169(3), 447-460.
- Doran, B. R., & Lewis, D.J. (2003). The species composition and seasonal distribution of mosquitoes in vernal pools in suburban Montreal, Quebec. *Journal of the American Mosquito Control Association*, 19(4), 339-346.
- Dyar, H. G. (1928). The mosquitoes of the Americas. Carnegie Institute of Washington Publication., No. 387. 616 pp.
- El Adlouni, S., Beaulieu, C., Ouarda, T. B., Gosselin, P. L., & Saint-Hilaire, A. (2007). Effects of climate on West Nile Virus transmission risk used for public health decision-making in Quebec. *International Journal of Health Geographics*, 6(1), 1.
- Ellis, A. M., Lounibos, L. P., & Holyoak, M. (2006). Evaluating the long-term metacommunity dynamics of tree hole mosquitoes. *Ecology*, 87(10), 2582-2590.
- Environment and Climate Change Canada (2015) The St. Lawrence River: Accessed August 2016. Retrieved from: <https://www.ec.gc.ca/stl/>
- Ewing, D. A., Cobbold, C. A., Purse, B. V., Nunn, M. A., & White, S. M. (2016). Modelling the effect of temperature on the seasonal population dynamics of temperate mosquitoes. *Journal of Theoretical Biology*, 400, 65-79.
- Favret, C., & Sieracki, J. M. (2016). Machine vision automated species identification scaled towards production levels. *Systematic Entomology*, 41(1), 133-143.
- Frank, J. H., & Lounibos, L. P. (2009). Insects and allies associated with bromeliads: a review. *Terrestrial Arthropod Reviews*, 1(2), 125-153.
- Ganser, C., & Wisely, S. M. (2013). Patterns of spatio-temporal distribution, abundance, and diversity in a mosquito community from the eastern Smoky Hills of Kansas. *Journal of Vector Ecology*, 38(2), 229-236.
- Giberson, D. J., Dau-Schmidt, K., & Dobrin, M. (2007). Mosquito species composition, phenology and distribution (Diptera: Culicidae) on Prince Edward Island. *Journal of the Acadian Entomological Society*, 3, 7-27.

- Ginsberg, H. S., Rochlin, I., & Campbell, S. R. (2010). The use of early summer mosquito surveillance to predict late summer West Nile virus activity. *Journal of Vector Ecology*, 35(1), 35-42.
- Godsey Jr, M. S., Burkhalter, K., Delorey, M., & Savage, H. M. (2010). Seasonality and time of host-seeking activity of *Culex tarsalis* and floodwater *Aedes* in northern Colorado, 2006–2007. *Journal of the American Mosquito Control Association*, 26(2), 148-159.
- Golding, N., Nunn, M. A., & Purse, B. V. (2015). Identifying biotic interactions which drive the spatial distribution of a mosquito community. *Parasites & Vectors*, 8(1), 1-10.
- Gong, H., DeGaetano, A. T., & Harrington, L. C. (2011). Climate-based models for West Nile *Culex* mosquito vectors in the Northeastern US. *International Journal of Biometeorology*, 55(3), 435-446.
- Gonsalves, L., Lamb, S., Webb, C., Law, B., & Monamy, V. (2013). Do mosquitoes influence bat activity in coastal habitats?. *Wildlife Research*, 40(1), 10-24.
- Gosselin, P., Lebel, G., Rivest, S., & Douville-Fradet, M. (2005). The Integrated System for Public Health Monitoring of West Nile Virus (ISPHM-WNV): a real-time GIS for surveillance and decision-making. *International Journal of Health Geographics*, 4(1), 1.
- Govella, N. J., Chaki, P. P., Mpangile, J. M., & Killeen, G. F. (2011). Monitoring mosquitoes in urban Dar es Salaam: evaluation of resting boxes, window exit traps, CDC light traps, Ifakara tent traps and human landing catches. *Parasites & Vectors*, 4(1), 1.
- Gubler, D. J. (2010). The global threat of emergent/re-emergent vector-borne diseases. *Vector Biology, Ecology and Control*. Springer. Netherlands. 260 pages.
- Guedes, M. L. P., & Navarro-Silva, M. A. (2014). Mosquito community composition in dynamic landscapes from the Atlantic Forest biome (Diptera, Culicidae). *Revista Brasileira de Entomologia*, 58(1), 88-94.
- Guinovart, C., Navia, M. M., Tanner, M., & Alonso, P. L. (2006). Malaria: burden of disease. *Current Molecular Medicine*, 6(2), 137-140.

- Haddow, A. D., Gerhardt, R. R., Jones, C. J., & Odoi, A. (2009). The mosquitoes of eastern Tennessee: studies on abundance, habitat preferences, and host-seeking behaviors. *Journal of Vector Ecology*, 34(1), 70-80.
- Halasa, Y. A., Shepard, D. S., Fonseca, D. M., Farajollahi, A., Healy, S., Gaugler, R., Bartlett-Healy, K., Strickman, D.A. & Clark, G. G. (2014). Quantifying the impact of mosquitoes on quality of life and enjoyment of yard and porch activities in New Jersey. *PloS ONE*, 9(3), e89221.
- Hamer, G. L., Donovan, D. J., Hood-Nowotny, R., Kaufman, M. G., Goldberg, T. L., & Walker, E. D. (2012). Evaluation of a stable isotope method to mark naturally-breeding larval mosquitoes for adult dispersal studies. *Journal of Medical Entomology*, 49(1), 61-70.
- Hamer, G. L., Anderson, T. K., Donovan, D. J., Brawn, J. D., Krebs, B. L., Gardner, A. M., Ruiz, M.O., Brown, W.M., Kitron, U.D., Newman, C.M., Goldberg, T. L. & Walker, E.D. (2014). Dispersal of adult *Culex* mosquitoes in an urban West Nile virus hotspot: a mark-capture study incorporating stable isotope enrichment of natural larval habitats. *PLoS Neglected Tropical Diseases*, 8(3), e2768.
- Hagstrum, D. W. (1971). Evaluation of the standard pint dipper as a quantitative sampling device for mosquito larvae. *Annals of the Entomological Society of America*, 64(3), 537-540.
- Hongoh, V., Berrang-Ford, L., Scott, M. E., & Lindsay, L. R. (2012). Expanding geographical distribution of the mosquito, *Culex pipiens*, in Canada under climate change. *Applied Geography*, 33, 53-62.
- Horsfall, W. R., Fowler Jr, H. W., Moretti, L. J., & Larson, J. R. (1973). Bionomics and embryology of the inland floodwater mosquito *Aedes vexans*. University of Illinois Press, Urbana, Ill. 211 pp.
- Howard, L. O., Dyar, H. G., & Knab, F. (1917). The mosquitoes of North and Central America and the West Indies: A general consideration of mosquitoes, their habits, and their relations to the human species (1912) 159 (4). Baltimore. Carnegie Institution of Washington. The Lord Baltimore Press.

- Hu, W., Tong, S., Mengersen, K., & Oldenburg, B. (2006). Rainfall, mosquito density and the transmission of Ross River virus: A time-series forecasting model. *Ecological Modelling*, 196(3), 505-514.
- Jacups, S. P., Carter, J., Kurucz, N., McDonnell, J., & Whelan, P. I. (2015). Determining meteorological drivers of salt marsh mosquito peaks in tropical northern Australia. *Journal of Vector Ecology*, 40(2), 277-281.
- Juliano, S. A., & Philip Lounibos, L. (2005). Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecology Letters*, 8(5), 558-574.
- Junglen, S., Kurth, A., Kuehl, H., Quan, P. L., Ellerbrok, H., Pauli, G., Nitsche, A., Nunn, C., Rich, S.M., Lipkin, W.I., Briese, T. & Leendertz, F.H. (2009). Examining landscape factors influencing relative distribution of mosquito genera and frequency of virus infection. *Ecohealth*, 6(2), 239-249.
- Kampen, H., & Werner, D. (2014). Out of the bush: the Asian bush mosquito *Aedes japonicus japonicus* (Theobald, 1901) (Diptera, Culicidae) becomes invasive. *Parasites & Vectors*, 7(1), 1.
- Kaufman, M. G., & Fonseca, D. M. (2014). Invasion biology of *Aedes japonicus japonicus* (Diptera: Culicidae). *Annual Review of Entomology*, 59, 31.
- Kilpatrick, A. M., Kramer, L. D., Jones, M. J., Marra, P. P., & Daszak, P. (2006). West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. *PLoS Biology*, 4(4), e82.
- Kilpatrick, A. M., Meola, M. A., Moudy, R. M., & Kramer, L. D. (2008). Temperature, viral genetics, and the transmission of West Nile virus by *Culex pipiens* mosquitoes. *PLoS Pathogens*, 4(6), e1000092.
- Kilpatrick, A. M. (2011). Globalization, land use, and the invasion of West Nile virus. *Science*, 334(6054), 323-327.
- Kingsolver, J. G. (1989). Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology*, 314-334.
- Koenraadt, C. J. M., & Harrington, L. C. (2008). Flushing effect of rain on container-inhabiting mosquitoes *Aedes aegypti* and *Culex pipiens* (Diptera: Culicidae). *Journal of Medical Entomology*, 45(1), 28-35.

- Lee, J. H., & Kokas, J. E. (2004). Field evaluation of CDC gravid trap attractants to primary West Nile virus vectors, *Culex* mosquitoes in New York State. *Journal of the American Mosquito Control Association*, 20(3), 248-253.
- Leprince, D. J., & Lewis, D. J. (1982). Relative abundance and seasonal distribution of adult mosquitoes in southern Quebec [*Mansonia perturbans*, *Aedes aurifer* and *Anopheles walkeri*]. *Mosquito News*, 42.
- Lysyk, T. J. (2010). Species abundance and seasonal activity of mosquitoes on cattle facilities in southern Alberta, Canada. *Journal of Medical Entomology*, 47(1), 32-42.
- Maire, A. (1982). Selectivity by six snow-melt mosquito species for larval habitats in Quebec subarctic string bogs. *Mosquito News*, 42(2), 236-243.
- Maleque, M. A., Ishii, H. T., & Maeto, K. (2006). The use of arthropods as indicators of ecosystem integrity in forest management. *Journal of Forestry*, 104(3), 113-117.
- Marfin, A. A., Petersen, L. R., Eidson, M., Miller, J., Hadler, J., Farello, C., Werner, B., Campbell, G. L., Layton, M., Smith, P., Bresnitz, E., Cartter, M., Scaletta, J., Obiri, G., Bunning, M., Craven, R. C., Roehrig, J. T., Julian, K. G., Hinten, S. R., Gubler, D. J. & the ArboNET Cooperative Surveillance Group (2001). Widespread West Nile virus activity, eastern United States, 2000. *Emerging Infectious Diseases*, 7(4), 730.
- Martens, W. J., Jetten, T. H., & Focks, D. A. (1997). Sensitivity of malaria, schistosomiasis and dengue to global warming. *Climatic Change*, 35(2), 145-156.
- Matheson, R. (1929). A handbook of the mosquitoes of North America. Bailliere, Tindall & Cox. London, 268 pp.
- McMahon, T. S., Galloway, T. D., & Anderson, R. A. (2008). Tires as larval habitats for mosquitoes (Diptera: Culicidae) in southern Manitoba, Canada. *Journal of Vector Ecology*, 33(1), 198-204.
- MSSS (2016) Ministère de la Santé et des Services sociaux: West Nile Virus (WNV). Accessed November 2016. Retrieved from: <http://sante.gouv.qc.ca/en/problemes-de-sante/virus-du-nil/>
- Norris, D. E. (2004). Mosquito-borne diseases as a consequence of land use change. *EcoHealth*, 1(1), 19-24.

- Opiyo, M. A., Hamer, G. L., Lwetoijera, D. W., Auckland, L. D., Majambere, S., & Okumu, F. O. (2016). Using stable isotopes of carbon and nitrogen to mark wild populations of *Anopheles* and *Aedes* mosquitoes in south-eastern Tanzania. *PloS ONE*, 11(7), e0159067.
- Paaijmans, K. P., Wandago, M. O., Githeko, A. K., & Takken, W. (2007). Unexpected high losses of *Anopheles gambiae* larvae due to rainfall. *PLoS ONE*, 2(11), e1146.
- Paaijmans, K. P., Imbahale, S. S., Thomas, M. B., & Takken, W. (2010). Relevant microclimate for determining the development rate of malaria mosquitoes and possible implications of climate change. *Malaria Journal*, 9(1), 1.
- Patz, J. A., Martens, W. J., Focks, D. A., & Jetten, T. H. (1998). Dengue fever epidemic potential as projected by general circulation models of global climate change. *Environmental Health Perspectives*, 106(3), 147.
- Patz, J. A., Campbell-Lendrum, D., Holloway, T., & Foley, J. A. (2005). Impact of regional climate change on human health. *Nature*, 438(7066), 310-317.
- Pecoraro, H. L., Day, H. L., Reineke, R., Stevens, N., Withey, J. C., Marzluff, J. M., & Meschke, J. S. (2007). Climatic and landscape correlates for potential West Nile virus mosquito vectors in the Seattle region. *Journal of Vector Ecology*, 32(1), 22-28.
- Pepin, K. M., Marques-Toledo, C., Scherer, L., Morais, M. M., Ellis, B., & Eiras, A. E. (2013). Cost-effectiveness of novel system of mosquito surveillance and control, Brazil. *Emerging Infectious Diseases*, 19(4), 542-50.
- Ponçon, N., Toty, C., L'ambert, G., Le Goff, G., Brengues, C., Schaffner, F., & Fontenille, D. (2007). Population dynamics of pest mosquitoes and potential malaria and West Nile virus vectors in relation to climatic factors and human activities in the Camargue, France. *Medical and Veterinary Entomology*, 21(4), 350-357.
- Pritchard, E. J. (2010). Seasonal abundance and distribution of mosquito species (Culicidae) in southwestern Quebec and their potential role as vectors of West Nile virus. In *Masters Abstracts International* 49(2).

- Quebec Energy and Natural Resources (2003) Overview of natural resources in the Montreal region. Accessed November 2016. Retrieved from:
<http://mern.gouv.qc.ca/english/montreal/overview/index.jsp>
- Reinert, J. F. (2000). New classification for the composite genus *Aedes* (Diptera: Culicidae: Aedini), elevation of subgenus *Ochlerotatus* to generic rank, reclassification of the other subgenera, and notes on certain subgenera and species. *Journal-American Mosquito Control Association*, 16(3), 175-188.
- Richards, S. L., Ghosh, S. K., Zeichner, B. C., & Apperson, C. S. (2008). Impact of source reduction on the spatial distribution of larvae and pupae of *Aedes albopictus* (Diptera: Culicidae) in suburban neighborhoods of a Piedmont community in North Carolina. *Journal of Medical Entomology*, 45(4), 617-628.
- Richards, E. E., Masuoka, P., Brett-Major, D., Smith, M., Klein, T. A., Kim, H. C., Anyamba, A., & Grieco, J. (2010). The relationship between mosquito abundance and rice field density in the Republic of Korea. *International Journal of Health Geographics*, 9(1), 1.
- Ritchie, S. A., & Kline, D. L. (1995). Comparison of CDC and EVS light traps baited with carbon dioxide and octenol for trapping mosquitoes in Brisbane, Queensland (Diptera: Culicidae). *Australian Journal of Entomology*, 34(3), 215-218.
- Rocheleau, J. P., Arsenault, J., Lindsay, L. R., DiBernardo, A., Kulkarni, M. A., Côté, N., & Michel, P. (2013). Eastern equine encephalitis virus: high seroprevalence in horses from southern Quebec, Canada, 2012. *Vector-Borne and Zoonotic Diseases*, 13(10), 712-718.
- Rochlin, I., Ninivaggi, D. V., Hutchinson, M. L., & Farajollahi, A. (2013). Climate change and range expansion of the Asian tiger mosquito (*Aedes albopictus*) in Northeastern USA: implications for public health practitioners. *PloS ONE*, 8(4), e60874.
- Roiz, D., Ruiz, S., Soriguer, R., & Figuerola, J. (2014). Climatic effects on mosquito abundance in Mediterranean wetlands. *Parasites & Vectors*, 7(1), 1.
- Rueda, L. M. (2008). Global diversity of mosquitoes (Insecta: Diptera: Culicidae) in freshwater. *Hydrobiologia*, 595(1), 477-487.

- Ruiz, M. O., Chaves, L. F., Hamer, G. L., Sun, T., Brown, W. M., Walker, E. D., Haramis, L., Goldberg, T. L., & Kitron, U. D. (2010). Local impact of temperature and precipitation on West Nile virus infection in *Culex* species mosquitoes in northeast Illinois, USA. *Parasites & Vectors*, 3(1), 1.
- Ryan, P. A., Lyons, S. A., Alsemgeest, D., Thomas, P., & Kay, B. H. (2004). Spatial statistical analysis of adult mosquito (Diptera: Culicidae) counts: an example using light trap data, in Redland Shire, southeastern Queensland, Australia. *Journal of Medical Entomology*, 41(6), 1143-1156.
- Rydzanicz, K., & Lonc, E. (2003). Species composition and seasonal dynamics of mosquito larvae in the Wroclaw, Poland area. *Journal of Vector Ecology*, 28, 255-266.
- Schäfer, M. L., Lundkvist, E., Landin, J., Persson, T. Z., & Lundström, J. O. (2006). Influence of landscape structure on mosquitoes (Diptera: Culicidae) and dytiscids (Coleoptera: Dytiscidae) at five spatial scales in Swedish wetlands. *Wetlands*, 26(1), 57-68.
- Schäfer, M. L., Lundström, J. O., & Petersson, E. (2008). Comparison of mosquito (Diptera: Culicidae) populations by wetland type and year in the lower River Dalälven region, Central Sweden. *Journal of Vector Ecology*, 33(1), 150-157.
- Schneider, D. W., & Frost, T. M. (1996). Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society*, 15(1), 64-86.
- Schneider, J., Valentini, A., Dejean, T., Montarsi, F., Taberlet, P., Glaizot, O., & Fumagalli, L. (2016). Detection of invasive mosquito vectors using environmental DNA (eDNA) from water samples. *PLoS ONE*, 11(9), e0162493.
- Schowalter, T. D. (2011). *Insect ecology: an ecosystem approach (3rd ed.)*. Academic Press. San Diego, California, USA.. 633 pp.
- Service, M. W. (1980). Effects of wind on the behaviour and distribution of mosquitoes and blackflies. *International Journal of Biometeorology*, 24, 347-353.
- Shaman, J., & Day, J. F. (2007). Reproductive phase locking of mosquito populations in response to rainfall frequency. *PLoS ONE*, 2(3), e331.

- Shand, L., Brown, W. M., Chaves, L. F., Goldberg, T. L., Hamer, G. L., Haramis, L., Kitron, E. D. & Ruiz, M. O. (2016). Predicting West Nile Virus infection risk from the synergistic effects of rainfall and temperature. *Journal of Medical Entomology*, 53(4), 935-944.
- Shililu, J., Ghebremeskel, T., Seulu, F., Mengistu, S., Fekadu, H., Zerom, M., Ghebregziabiher, A., Sintasath, D., Bretas, G., Mbogo, C., Githure, J., Brantly, E., Novak, R., & Beier, J. C. (2003). Larval habitat diversity and ecology of anopheline larvae in Eritrea. *Journal of Medical Entomology*, 40(6), 921-929.
- Silver, J. B. (2008). *Mosquito ecology: field sampling methods* (3rd ed.). Springer Science & Business Media. New York, NY. 1477 pp.
- Singer, R. B. (2001). Pollination biology of *Hebenaria parviflora* (Orchidaceae: Habenariinae) in southeastern Brazil. *Darwiniana*, 39(3), 201-207.
- Speight, M. R., Hunter, M. D., & Watt, A. D. (1999). *Ecology of insects: concepts and applications*. Blackwell Science Ltd. Malden, MA, USA. 350 pp.
- Stein, M., Santana, M., Galindo, L. M., Etchepare, E., Willener, J. A., & Almirón, W. R. (2016). Culicidae (Diptera) community structure, spatial and temporal distribution in three environments of the province of Chaco, Argentina. *Acta Tropica*, 156, 57-67.
- Thielman, A., & Hunter, F. F. (2006). Establishment of *Ochlerotatus japonicus* (Diptera: Culicidae) in Ontario, Canada. *Journal of Medical Entomology*, 43(2), 138-142.
- Thielman, A. C., & Hunter, F. F. (2007). *A photographic key to adult female mosquito species of Canada (Diptera: Culicidae)*. Canadian Journal of Arthropod Identification, 4, 1-117.
- Trewin, B. J., Kay, B. H., Darbro, J. M., & Hurst, T. P. (2013). Increased container-breeding mosquito risk owing to drought-induced changes in water harvesting and storage in Brisbane, Australia. *International Health*, 5(4), 251-258.
- Turell, M. J., Dohm, D. J., Sardelis, M. R., O'guinn, M. L., Andreadis, T. G., & Blow, J. A. (2005). An update on the potential of North American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. *Journal of Medical Entomology*, 42(1), 57-62.

- USDA (2016) United States Department of Agriculture: USDA Engages Public through Crowdsourcing and Citizen Science. Accessed November 2016. Retrieved from: <http://blogs.usda.gov/2016/04/15/usda-engages-public-through-crowdsourcing-and-citizen-science/>
- van den Hurk, A. F., Hall-Mendelin, S., Johansen, C. A., Warrilow, D., & Ritchie, S. A. (2012). Evolution of mosquito-based arbovirus surveillance systems in Australia. *BioMed Research International*, 2012 (2).
- van den Hurk, A. F., Hall-Mendelin, S., Townsend, M., Kurucz, N., Edwards, J., Ehlers, G., Rodwell, C., Moore, A., McMahon, L., Nothill, A., Simmons, R. J., Cortis, G., Melville, L., Whelan, P.I., & Ritchie, S. A. (2014). Applications of a sugar-based surveillance system to track arboviruses in wild mosquito populations. *Vector-Borne and Zoonotic Diseases*, 14(1), 66-73.
- Wilkerson, R. C., Linton, Y. M., Fonseca, D. M., Schultz, T. R., Price, D. C., & Strickman, D. A. (2015). Making mosquito taxonomy useful: a stable classification of tribe Aedini that balances utility with current knowledge of evolutionary relationships. *PLoS ONE*, 10(7), e0133602.
- Williams, C. R., Long, S. A., Webb, C. E., Bitzhenner, M., Geier, M., Russell, R. C., & Ritchie, S. A. (2007). *Aedes aegypti* population sampling using BG-Sentinel traps in north Queensland Australia: statistical considerations for trap deployment and sampling strategy. *Journal of Medical Entomology*, 44(2), 345-350.
- Williams, P., Biggs, J., Fox, G., Nicolet, P., & Whitfield, M. (2010). History, origins and importance of temporary ponds. *Freshwater Forum* 17(1).
- Wood, D. M., Dang, P. T., & Ellis, R. A. (1979). The insects and arachnids of Canada. Part 6. The mosquitoes of Canada. Diptera: Culicidae. Canadian Government Publishing Centre. Hull, Quebec. 390 pp.
- Williams, G. M., & Gingrich, J. B. (2007). Comparison of light traps, gravid traps, and resting boxes for West Nile virus surveillance. *Journal of Vector Ecology*, 32(2), 285-291.
- Yan, Z. C., & Zhong, H. (2005). Comparison of adult mosquito community structure on various habitats. *Insect Science*, 12(3), 193-197.

- Yee, D. A. (2008). Tires as habitats for mosquitoes: a review of studies within the eastern United States. *Journal of Medical Entomology*, 45(4), 581-593.
- Yee, D. A., Kneitel, J. M., & Juliano, S. A. (2010). Environmental correlates of abundances of mosquito species and stages in discarded vehicle tires. *Journal of Medical Entomology*, 47(1), 53-62.
- Yi, H., Devkota, B. R., Yu, J. S., Oh, K. C., Kim, J., & Kim, H. J. (2014). Effects of global warming on mosquitoes & mosquito-borne diseases and the new strategies for mosquito control. *Entomological Research*, 44(6), 215-235.
- Zhong, H. E., Yan, Z., Jones, F., & Brock, C. (2003). Ecological analysis of mosquito light trap collections from West Central Florida. *Environmental Entomology*, 32(4), 807-815.

1.9 Connecting Statement

Chapter 1 outlined the rationale and specific objectives for this thesis. It provided the background information and context for the research appearing in the two subsequent chapters. Chapter 2 examines the effect of habitat in shaping mosquito communities across three common habitat types found in the region, these being suburban, field and forest habitat. It also explores specific patterns of abundance, species richness, shared species, and the relative abundance of dominant species, all within the context of habitat.

Chapter 2: The diversity and community structure of mosquitoes (Diptera: Culicidae) in suburban, field, and forest habitats in Montréal (Canada)

2.1 Introduction

Mosquitoes (Diptera: Culicidae) are medically, economically and ecologically important flies that live in most terrestrial habitats. In addition to being nuisance pests (Dickinson & Paskewitz, 2012; Halasa et al., 2014), and vectors of disease (Gubler, 1998; Norris, 2004; Rochlin et al., 2013), mosquitoes also provide essential ecosystem services such as pollination (Singer, 2001; Döetterl et al., 2012), and are prey for highly valued vertebrates (Rueda, 2008; Gonsalves et al., 2013). Although there has been considerable effort to identify and document the range and biology of mosquito species across North America (Juliano & Lounibos, 2005; Pecoraro et al., 2007; Haddow et al., 2009; Andreadis & Wolfe, 2010; Buckner et al., 2011; Ganser & Wisely, 2013), the exact distribution and habitat preferences of most species are still not entirely known. Improving our knowledge of Culicid populations requires that we study their ecology in detail (Alencar et al. 2015). Many species of mosquitoes tolerate and are adaptable to a broad range of landscape and environmental conditions, which allows them to survive just about anywhere (Barrera & Medialdea, 1996; Chase & Knight, 2003; Medlock et al., 2012). Despite potentially extreme differences in microclimate or resource availability, many species, including those which pose serious health risks, can be found over a wide range of different habitat types (Pecoraro et al., 2007; Abella-Medrano et al., 2015; Medlock & Vaux, 2015). Across a habitat gradient, populations of different species can overlap, leading to a community continuum of shared species and similarity in community structure (Whittaker, 1972). Species sharing between disparate habitat types means that taxa of significant medical or economic importance can be found in many different areas. By identifying the degree of sharing and the dominant species composition of habitats, targeted management and surveillance strategies can be designed with greater effectiveness. Landscape management and infrastructure planning can be designed for greater safety if species of known health risk are incorporated into the surveillance and monitoring design.

Mosquito communities are not distributed uniformly in a given landscape, either temporally or spatially, due in part to environmental conditions, habitat variability, ability to disperse and host-seeking behavior (Zhong et al., 2003, Kilpatrick et al., 2006, Sérandour et al., 2010). In recent years, due in particular to a rise in the number of arbovirus epidemics and the spread of competent vector species around the globe (Juliano & Lounibos, 2005; Lambrechts et al., 2010; Benelli & Mehlhorn, 2016; Fauci & Morens, 2016), much research exists into factors driving these events (Stoddard et al., 2009; Duncombe et al., 2013; Roche et al., 2015). Knowledge of mosquito communities and how this relates to habitat type, particularly in areas with human presence, is important for understanding nuisance potential and the risk of disease transmission. It allows us to identify habitat usage for species implicated as important biting pests or disease vectors (Molyneux et al., 2008; Chaves et al., 2010; Johnson et al., 2012; Guedes & Navarro-Silva, 2014) and allows streamlining of mosquito control measures at narrow landscape scales. In a recent study, Halasa et al. (2014) found that nuisance behaviour of biting mosquitoes limited the amount of time people spend outdoors, doing recreational activities, or simply enjoying their yards. The West Island of Montreal is an important area to study with regard to mosquito distribution, as it is composed of several large and interconnected green spaces, ecological reserves and agricultural land adjacent to suburban communities and a large human population.

The primary objective of this research is to determine the role of habitat in shaping mosquito community structure by comparing three dominant habitat types found on the western part of the island of Montréal: forests, fields and suburban backyards. A second objective is to address specific patterns of abundance, species richness and species sharing between habitat types, and a third to assess within-habitat differences in species-specific patterns of dominance.

2.2 Methods

2.2.1 Study Sites

Sampling locations were located near the western tip of the island of Montréal in Québec, Canada (45° 31' N, 73° 34' W). This area is characterized by suburban communities with numerous interspersed green spaces, wetlands and agricultural areas. It is situated in the Great Lakes - St. Lawrence Lowlands ecotype, an area which has experienced much human alteration and is home to a large portion of the Canadian population (El Adlouni et al., 2007; Parks Canada, 2009).

Twenty sampling locations were chosen across different habitat types (Fig. 2.1). Habitat types comprised three broad categories, defined as “suburban” characterized by single family housing with parks, trees, and adjacent green spaces, “forest” comprising large overstory trees, and “fields”, open areas lacking tree cover and composed mostly of low growing herbaceous vegetation or agricultural crops. At least three replicate locations were sampled for each habitat type. Three locations were sampled in each of two suburban municipalities (Baie d’Urfé (BDU) and Sainte-Anne-de-Bellevue (SADB)). Forested habitats were located within the Morgan Arboretum, a 245 ha forested property located within the town of Sainte-Anne-de-Bellevue. Three forest types, distinguished by dominant overstory tree species composition (Sugar Maple (*Acer saccharum*) (SM), American Beech-Red Maple (*Fagus grandifolia*/*Acer rubrum*) (BRM) and Eastern Hemlock (*Tsuga canadensis*) (HEM)) were studied, each receiving three traps, with the exception of Sugar Maple which received four. Four field locations were chosen, each receiving a single trap.

2.2.2 Sample collection and specimen processing

Mosquitoes were sampled weekly from 25 June to 1 October in 2014, and from 19 April to 14 October, 2015, for a total of 15 and 25 sampling weeks per year, respectively. Traps were serviced once a week for a total of 300 and 500 trap collections for 2014 and 2015, respectively. Traps used were All-weather LED EVS traps (Bioquip Products, Inc® Rancho Dominguez, CA) baited with 1.5 kg of dry ice and suspended 1.5 m above the ground. Traps were deployed early afternoon and remained open for 24h to sample

in all activity periods (i.e., daylight, crepuscular, night). After 24h, trap bags were removed and specimens placed into the freezer for later identification.

Identification was done with the use of keys to morphological characters (Wood et al., 1979, Darsie & Ward, 2005; Thielman & Hunter, 2007). All adult female specimens were identified to species and counted in the samples from each collected trap. If a specimen was too damaged to identify to species it was counted but left as unknown. The naming and abbreviations used herein for all genera follow the classification outlined by Wilkerson et al. (2015). Voucher specimens of all species are deposited at the Lyman Entomological Museum, McGill University (Ste-Anne-de-Bellevue, Québec, Canada).

2.2.3 Trapping considerations

We recognize that sampling across distinct habitat types creates a situation where the habitat itself can alter the capture rates of mosquitoes. For instance, light traps located in field habitat will be more visible to questing adult females at longer distances than those in forested habitat. This may lead to an overestimation of abundance in field habitat, or potentially underestimating in forested habitats. Within suburban habitat, competing light sources (porch lights, street lights, etc.) (Barghini & De Medeiros, 2010) and different sources of CO₂ (vehicles, people, etc.) may result in dilution of mosquitoes attracted to baited light traps. Although hard to quantify, these sources of error are likely occurring at large scales and the micro scale and should be given consideration in the future.

2.2.4 Data analyses

To test the effect of habitat on shaping mosquito community structure, and to visualize this relationship, nonmetric multidimensional scaling (NMDS) ordinations were generated using the function metaMDS in vegan library version 2.2-1 (Oksanen, 2015) in R version 3.1.3 (R Development Core Team 2015). Detailed discussion of this method and its application in the analysis of ecological communities can be found in several works (Clark, 2005; Holland, 2008; Rossi, 2010). Mosquito data were pooled by location (e.g., BDU, Field, SM, etc.) and by year. All data were square root transformed

to reduce the effect of very abundant species. To aid in interpretation, the *ordiellipse* function was used to superimpose the SE with 95% confidence limit as an indication of significance between sites. The significance of the interaction between habitat types was determined using a permutational multivariate analysis of variance (PERMANOVA) using distance matrices, followed by Bonferroni Multiple Comparison Test to perform a pairwise comparison across all habitats for each year.

Sample data from each location were pooled by year and the locations were assigned to their respective habitat type for analysis. Subsequently, ANOVA tests were performed to identify the effect of the different locations on abundance (log +1 transformed) and species richness (total observed species). Analysis of variance was followed by Tukey HSD (Honest Significant Difference) for pairwise comparisons. Tests were performed using the functions *aov* and *TukeyHSD* in R version 3.1.3 (R Development Core Team 2015).

Habitats were further compared by analysing the total abundance as well as total, unique, and shared species for each of the three broad habitat types. Species accounts are based on presence/absence observations and singleton species were considered in this comparison. Shared species were used to highlight similarities between the three habitat types with respect to their overall richness.

Mean abundance (mean number of individuals per trap) and species richness were calculated for each site. Mean number of mosquitoes per site was calculated by dividing the total number of mosquitoes collected in each site by the number of trap collections. This provides a better indication of abundance than comparing raw abundance between habitats, as there were an unequal number of trap replicates. Species richness was determined as the total number of species captured at each site and included singleton species. Quantifying species richness allows comparisons among different sites and allows sampling efficiency to be assessed. Comparisons of species richness across different spatial or temporal scales is difficult when sampling effort is not equal, as in this study. Therefore, individual-based rarefaction estimates were generated to

standardize the richness values to a sample size that is comparable across all sampling units (Buddle et al., 2005). Rarefaction estimates for each site were produced using the rarefy function in vegan library version 2.2-1 (Oksanen, 2015) in R version 3.1.3 (R Development Core Team 2015) to generate extrapolated values beyond the observed species richness at each site. To allow direct comparison of species richness across the two seasons, a truncated version of the 2015 data was generated by removing all weeks which were not sampled in both years. The number of sample weeks was reduced from 25 to 15 to mirror the sampling effort in the previous year. Rarefy was again run for this truncated data subset.

Patterns of species dominance were generated by comparing rank abundance in each year and selecting the five most abundant species encountered based on total abundance for each site. Dominant species generally made up >5% of the total catch in a given year (Rydzanicz & Lonc, 2003 – adapted from Trojan (1992)) and the five highest ranked species were selected (Burkett-Cardena et al., 2008; Lysyk, 2010) as well as the medically important *Culex pipiens* (L.). Relative proportions were calculated with regards to these species alone.

2.3 Results

2.3.1 General results

A total of 184,607 mosquitoes was collected in the two study years, with 43,443 specimens in 2014 and 141,164 in 2015. These represented 35 species (29 in 2014, 34 in 2015) in 8 genera (Table 2.1). The genus *Aedes* had the most species (21); three species (*Aedes vexans* (39%), *Coquilleltidia perturbans* (18%), and *Aedes canadensis* (16%)) comprised nearly 75% of the total number of mosquitoes collected across both sampling seasons (Table 2.1).

One species collected during this study was not known previously from the province of Quebec. *Psorophora ferox* (Humboldt) (Wood et al., 1979; Darsie & Ward, 2005) was observed as 32 individuals in 2014 increasing to 652 in 2015 with several males also collected. This species is showing evidence of range expansion and a well-established

population, and as such we suggest it receive recognition as a newly established species in the province of Quebec.

2.3.2 Community structure

As revealed by NMDS ordination, community structure was distinct across the habitat types for both years (Fig. 2.2). The mosquito communities showed clear separation between the habitat types as seen by the relative distance observed between the sampling sites in the ordination space. This suggests that community structure is dissimilar. The ellipses which constrain each set of associated points show the standard error (SE) about the mean. The lack of overlap between the observed means suggests dissimilarity. PERMANOVA results (Table 2.2) illustrate that habitats showed significant variation when analyzed using Bonferonni multiple comparison tests on pair-wise habitat groups, all were significantly different with the exception of suburban compared to field habitats in 2015 (Table 2.2). Within the habitat types, the sites showed little variation as seen by the overlap in sample means (Fig. 2.2); this is especially evident when comparing forest and suburban sites.

2.3.3 Abundance and richness

Across both sampling seasons, the highest mean abundances per trap were collected in field habitat and the lowest in suburban areas (Fig. 2.3). Mean number of mosquitoes per trap was much higher in 2015, related to the 3-fold increase in total mosquitoes collected compared to 2014 (Table 2.1). Species richness per site demonstrated an increase along a disturbance gradient with the lowest values found in suburban areas and increasing incrementally to fields and finally reaching highest values in forested sites (Fig. 2.4). This pattern was exhibited in both years. Rarefied species richness shows that the expected number of species was highest in BDU in 2014 and highest in HEM in 2015 for both the full data set and the truncated subset which mirrors the same sampling period in 2014 (Appendix 2.1). All rarefied estimates based on the lowest number of individuals collected at a given site in each year were lower than the actual number of species collected at each site, suggesting that overall, sites were sampled adequately. The municipality of BDU contained the lowest number of individuals

collected in all three generated rarefaction estimates and was used as the basis for comparison.

When tested using an ANOVA for significance using “site” as a factor in both years, abundance and richness were both significant ($P < .05$) (Table 2.3). When tested individually using pair-wise comparisons (Tukey HSD) between sites, abundance and species richness varied. BDU-SADB interactions and the interactions between all forested sites were not significant. The results support that patterns observed with ordination in comparing suburban sites and forest sites do not generate any significant differences in abundance or observed richness with pair-wise comparisons (Table 2.3).

Overall abundance and species richness varied between habitat types (Fig. 2.5): in both 2014 and 2015, suburban areas showed the lowest total abundance. Total abundance was highest in forested habitat in 2014 and in field habitat in 2015. Forested sites in both years had the highest species richness and suburban sites consistently had the lowest. In both years, fields had higher species richness than suburban habitat but less than forested habitat. This clearly demonstrates increasing species richness across a habitat gradient from suburban to field and forests.

2.3.4 Shared species

The number of shared species in both years was highest between forest and field habitat and lowest between field and suburban habitat (Fig. 2.5). Suburban habitat in general showed a greater number of shared species with forests than fields. Nearly 52% of all species encountered were shared between the three habitat types in 2014, and this number climbed to almost 65% in 2015. Forest habitats generated the highest number of unique species in each year with three in 2014 (equal to fields) and two in 2015.

2.3.5 Relative Abundance of selected species

Habitat differences were observed with respect to relative abundance of dominant species in both years (Fig. 2.6). All species occurred in every site; however, some were

present in such low numbers that their relative proportion was equal to <1% and did not contribute greatly to this dominance matrix.

In 2014, *Ae. vexans* dominated in suburban habitats and all other species had a relatively similar, but lower relative abundance. Field habitat was co-dominated by *Ae. vexans* and *Cq. perturbans* with other species scarcely represented. Forested sites were clearly the preferred habitat for *Ae. canadensis* with over 60% representation across all three sites. *Ae. trivittatus* and *Ae. stimulans* occurred in low densities in all habitats with highest relative abundance in suburban sites

In 2015, suburban sites were once again dominated by *Ae. vexans*, but to an even higher degree than in 2014. Field habitat was again co-dominated by *Ae. vexans* and *Cq. perturbans* but with the former having higher relative abundance. Forested sites remained the most suitable habitat for *Ae. canadensis* but with lower relative abundance than 2014. *Ae. trivittatus* was found in much higher relative abundance in forested sites compared to 2014. *Ae. provocans* showed a clear preference for forested sites with higher representation in BRM and HEM compared to SM.

Cx. pipiens showed strong association to the more disturbed areas, being found in greatest total numbers in suburban sites followed by fields. Their occurrence in forested habitats was almost negligible; HEM generated the greatest total catches with 5 individuals in 2014 and 37 in 2015.

2.4 Discussion

Mosquitoes are abundant and widely distributed around the world with unparalleled medical and economic importance as pests and vectors of disease, and yet the structure of mosquito communities, especially in Canada, has been poorly studied. Our research compared mosquito communities among three dominant habitats on the island of Montreal, with the goal of identifying how mosquito communities are structured in relation to habitat type and how mosquito abundance, richness, species sharing and

dominance varied between the studied sites. Our study design used systematic sampling across two years in three distinct habitat types across a suburban to forest gradient.

2.4.1 Habitat in shaping community structure

The multivariate analyses clearly illustrate the effects of habitat on shaping the community structure of mosquitoes: field, suburban, and forested habitats supported distinct assemblages of mosquitoes (Fig. 2.2). The only exception was the community structure of suburban and field habitats in 2015 which was not significantly different ($P=.075$) (Table 2.2). The similarities observed here are likely due to a greater increase in the number and richness of mosquitoes collected in suburban areas in 2015. Within-habitat differences (e.g., between multiple forest types) were much less pronounced, suggesting that like-habitats can support similar mosquito communities. This result reinforces the importance of habitat type in shaping mosquito communities, a finding that is consistent with the literature. Studies suggest that habitat is ultimately the main driver in determining community structure, although between-habitat similarities may still exist (Zhong et al., 2003; Yan & Zhong, 2005) as we observed here.

Recent studies examining the effect of disturbance gradients (urban-rural) revealed that communities vary with habitat type, and that abundance and species richness tend to increase along the gradient from anthropic disturbance to more pristine environments (Rochlin et al., 2008; Stein et al., 2016). Our study revealed similar trends. Alencar et al. (2015) found site to be significant in structuring communities and argue that a likely driver of these community level differences is habitat structure and the availability of breeding sites. This linkage of habitat type to the availability of breeding sites and the resulting mosquito community structure has been observed in other works (Ganser & Wisely, 2013; Golding et al., 2015). Successful development of larvae is tied not only to the availability of breeding sites, but also to smaller, habitat-driven qualities of these habitats, including water quality, light intensity, organic inputs, temperature and biotic interactions, factors which vary by location and habitat complexity at small geographic scales (Becker et al., 2003; Kling et al., 2007; Juliano, 2009; Fader & Juliano, 2014).

Smith et al. (2004) modelled the density of adult mosquitoes and demonstrate declines with distance from breeding sites, and suggest that if habitat is suitable and potential hosts are abundant, mosquitoes will restrict their movements. This can be seen by the distribution of *Cx. pipiens* which shows preference for suburban habitat and is not commonly encountered in more natural habitats. Others however, such as *Ae. vexans* and *Cq. perturbans* were found in high density, in all habitats, whether or not they contain ideal breeding locations, suggesting that dispersal from breeding sites is likely species specific.

Habitat preference of species can play a role in shaping communities, especially at the scale of like-habitats where no significant dissimilarity was observed in this study. When species show a distinct preference for a given habitat, their presence and relative proportions may alter the results of community comparisons. Howard et al. (1983) determined that most of the species they encountered showed distinct preference for a single habitat type, thus reducing the similarity in community structure compared across multiple habitat types. For instance, forest habitat is distinctly different from the other habitat types but different forest sites are quite similar. Species like *Ae. canadensis*, which clearly show habitat preference for forested sites, are likely responsible for these patterns.

2.4.2 Abundance

We quantified adult mosquito abundance by evaluating the mean number of adults collected per trap and compared these values across all six sites (Fig. 2.3). Our results indicate a higher number of trap visits in open field habitat compared to either suburban or forested sites. This finding is consistent with the work of Steiger et al. (2012) who collected a greater abundance of mosquitoes in grassland habitat compared to forest interior and edge habitat. Light emitted from traps located in field sites would be visible from longer distance and from all sides. Early work on long range visual orientation by mosquitoes demonstrated that females will disperse to different areas in response to stimuli like traps or hosts (Bidleingmayer & Hem, 1981). The ability of individual species to locate traps and their ability to disperse from source areas has been shown to

influence species distributions and abundance (Schowalter, 2011). Short to long range wind dispersal allows mosquitoes to locate hosts or breeding sites (Service, 1980; Cummins et al., 2012) except for container breeding species, which have more limited dispersal distance (Bellini et al., 2010; Hamer et al., 2014). Traps in open areas are likely to produce large amounts of questing adult females. Field captures comprised mainly *Ae. vexans* and *Cq. perturbans*, species known to travel long distance in search of suitable hosts (Cupp et al., 2003, Turell et al., 2005, Abella-Medrano et al., 2015). Overall, abundance was much higher in 2015 compared to 2014 across all habitats and this is likely a reflection of the nearly 3-fold increase in the number of mosquitoes collected in 2015 (Table 2.1).

2.4.3 Richness

Our study demonstrates an increase in species richness along a habitat gradient from suburban-forest habitats (Fig. 2.4; Fig. 2.5). Reasons for this could be increased structural complexity in forests, which may provide a wider range of breeding opportunities and a greater density of hosts (Tews et al., 2004; McElhinny et al., 2005; Johnson et al., 2012). Stein et al. (2016) found that semi-urban and pristine wild areas contained the greatest richness of species compared to more human altered environments. Zhong et al. (2003) and Johnson et al. (2008) also found an increase in species richness with increasing habitat complexity, as these habitats offer a variety of landscape features with increased structure. Poppe et al. (2015) argue that forests also offer greater stability than other, more disturbed sites. Field habitat showed greater diversity than suburban sites possibly due to its proximity to forested habitats relative to suburban areas (Fig. 2.1). Although the suburban areas were more favorable for container breeding species like *Cx. pipiens* and the invasive rock pool mosquito *Ae. japonicus* (Theobald), these species were also detected in low numbers in other habitats. Conversely, a greater number of species occurred in forested areas that were not detected in suburban yards. Rarefaction estimates of species richness suggest that all sites were adequately sampled due to the fact that the estimated species richness was lower than the total number of species actually collected at each site (Appendix 2.1; Fig 2.4). This also means that if sampling effort was standardized to that of the

suburban areas, total species richness at all other locations would have been lower. Truncating the values for 2015 to mirror the same sampling period for 2014 did not alter the trends of species richness of the rarefied estimates.

2.4.4 Shared species

Studies of community ecology often rely on spatial occurrence of species in simple presence/absence matrices to draw conclusions about community dynamics (MacKenzie et al., 2004). Here we compare the distribution of species across different habitat types and reveal patterns of species co-occurrence, unique species and total abundance (Fig. 2.5). Several of the species found in each habitat type were represented in low numbers, which may be indicative of incidental captures outside the normal habitat preferences of a given species. When comparing tropical forest habitat to more disturbed habitats, Steiger et al. (2012) found that half of their species occurred in all habitat types, with few habitat specialists, a finding similar to ours (Fig. 2.5; Fig. 2.6). Similarly, Abella-Medrano et al. (2015) noted a high degree of species sharing between sites with different land-uses, and similarly again to this study, they found that abundance was highly variable, suggesting that resource availability varies across space and time shaping distribution. Close proximity of the sampling locations in this study likely resulted in a higher degree of species sharing. Despite the structural differences experienced in each of the habitat types, the attractiveness of CO₂ baited light traps likely drew species from a greater distance and from a diversity of surrounding habitats (Bidlingmayer & Hem, 1981).

Changes were seen at the level of overall abundance, with forests having the highest observed abundance in 2014 and fields having greater abundance in 2015 (Fig. 2.3). This difference is likely tied to changes in abundance of a single species, *Ae. vexans*, which experienced a dramatic increase in abundance from 2014 to 2015 (Table. 2.1, Fig. 2.6), a trait well known of this species (Wood et al., 1979). Seasonal fluctuation in mosquito communities can vary annually, resulting in changes to overall abundance and community structure. This is likely related to environmental conditions which fluctuate from year to year (Lysyk, 2010; Buckner et al., 2011; Ganser & Wisely, 2013). Despite

changes in overall mosquito numbers, patterns of species richness remained the same each year, increasing consistently from suburbs, fields, and forests (Fig. 2.5).

It is possible that forests provide a more stable habitat for mosquitoes which may result in greater richness and create a greater degree of specialization as it does with some Diptera (Poppe et al., 2015). The degree of species sharing showed similar trends across both years (Fig. 2.6). Forest and field habitats consistently had the highest number of shared species, whereas suburbs and fields had the lowest. An interesting observation is that suburban yards had the greatest number of shared species with forested habitat despite suburbs having the lowest number of recorded species, and forests, the highest. This may be indicative of the importance of vertical structure in determining habitat preference, as both these habitats contain trees, a characteristic not found in field habitat. Trees offer a variety of breeding opportunities in the form of tree holes, a particular habitat known to be used by a multitude of species (Wood et al., 1979; Bradshaw & Holzapfel, 1992; Srivastava & Lawton, 1998). Several new species were added to the suburban sites in 2015, particularly Sainte-Anne-de-Bellevue, which saw a marked increase from 18 species in 2014 to 26 in 2015.

2.4.5 Relative abundance of selected species

Many species may compose a community, but abundance will vary, with some species being very common (dominants) and others moderately abundant or rare (Whittaker, 1965). Dominant species are an important consideration when comparing mosquito communities as the dominant species contribute greatly to shaping the community structure and reveal patterns of nuisance and vector potential (Meide et al., 2008; Guedes & Navarro-Silva, 2014). Similar species dominated the total catch in both sampling years and our findings reveal that species dominance is dependent on habitat type (Fig. 2.6). Of the dominant species encountered in both years, four species clearly had the highest abundance, these being *Ae. vexans* (Meigen), *Cq. perturbans* (Walker), *Ae. canadensis* (Theobald) and *Ae. trivittatus* (Coquillett) (Table 2.1.; Fig 2.6). This pattern of species dominance was also observed by Abella-Medrano et al. (2015) who found that dominance was always attributed to four species regardless of site. Within

sites derived from similar habitat, for example, those of the suburban and forest sites, patterns of dominance are maintained (Fig 2.6). These sites show similar proportions of the same species, a notion supported by (MacArthur, 1960), who showed that the likelihood of common species being found between similar habitats is high.

All species considered dominant in this study were encountered in all sites, but their relative proportion (i.e., dominance) varied. Within suburban sites, *Ae. vexans* contributed the greatest number of individuals. This species breeds in a variety of habitats and can reach very high numbers following periodic rain events (Wood et al., 1979, Crans, 2004). Because of this, it appears in high numbers across all habitat types, an observation also made by Shone et al. (2001). Suburban sites also produced large numbers of *Ae. stimulans* in 2014 and *Ae. trivittatus* in 2015. Field habitat was dominated by two principal species, *Ae. vexans* and *Cq. perturbans*. Both species are known to frequent open area habitats (Carpenter & Lacasse, 1955; Howard et al., 1983; Bosak et al., 2001). Forested sites contained large numbers of *Ae. canadensis*, a species known to breed in shaded woodland pools or mixed woodland habitat (Carpenter & Lacasse, 1955; Wood et al., 1979; Nasci et al., 2000). The relative abundance of this species varied between years, with much higher proportions collected in 2014. This is likely a result of the extended sampling season in 2015 which collected much higher numbers of *Ae. trivittatus* and *Ae. provocans*, two species which generally emerge earlier in the season compared to *Ae. canadensis* (Wood et al., 1979) and would have been under sampled in 2014. A main difference to note is the replacement of *Ae. stimulans* in 2014 with *Ae. provocans* in 2015 to the list of dominant species. Again, this is likely related to earlier sampling in 2015, which would have produced larger numbers of *Ae. provocans*. Thus, species dominance varies with habitat type, yet similarities exist when comparing sites of similar overall structure. The differences observed between years suggest that, to create a better representation of species and their relative proportions, sampling should begin at the earliest date possible within a given region. Samples may also be analysed by month or week to identify patterns over distinct temporal intervals.

2.4.6 Vector ecology

The distribution of *Culex pipiens* across habitat types is integral to our understanding of local vector ecology due to the medical importance of this species in the transmission of WNV (Andreadis et al., 2001; Turell et al., 2005). The comparison of species dominance by site (Fig. 2.6) shows that this species occurs mainly in suburban sites with few individuals (typically <1%) collected elsewhere. Studies examining the habitat preferences of *Cx. pipiens* demonstrate a close association with disturbed habitats such as urban and suburban areas (Kling et al., 2007; Pecoraro et al., 2007; Junglen et al., 2009; Johnson et al., 2012) and that this species will readily use, and may even prefer, artificial breeding sites associated with peridomestic water sources (Norris, 2004; Yee, 2008; Deichmeister & Telang, 2011). Our findings suggest that suburban areas are likely an important source of *Culex* mosquitoes and that programmes to combat West Nile virus should focus on these habitats. Although *Culex* spp. are often considered the primary WNV vectors, it should be noted that many others encountered during this study, including the five most abundant species, have shown to be carriers for WNV but with varied vector competence (Turell et al., 2005; CDC, 2012).

2.4.7 Conclusions

Our findings suggest that habitat plays an important role in shaping mosquito community structure and species interactions. Across the three broad habitat types sampled during this study, community structure is distinct, and this pattern was maintained in both years. Sites which contain similar structural components such as those in multiple forest types or suburban municipalities show a higher degree of similarity in their overall mosquito communities. Habitats with different structural elements (i.e., suburban vs. field vs. forest) vary with respect to community structure, dominance, and abundance with few exceptions. Natural forested habitats and adjacent fields can support a greater diversity of species and greater abundance of mosquitoes compared to suburban habitat. Many of the species encountered throughout this study can be found in all habitats sampled, suggesting a high number of generalists, whereas some, particularly the dominant species, show a degree of habitat preference.

Cx. pipiens, a medically important species in the transmission cycle of WNV shows greater preference for suburban habitat. This study provides information about the distribution and abundance of mosquito species in a heterogeneous landscape, which, when coupled with knowledge of phenology and natural history, provide insight into the nuisance potential and likelihood of disease transmission perpetuated by mosquitoes. The close association between suburban habitats and the proliferation of *Cx. pipiens* is an important finding with respect to WNV surveillance and management in the province of Quebec. We also describe the detection of a new species record for the province, emphasising the need for routine mosquito monitoring in as many different areas as possible. Further studies are needed to examine mosquito community structure at larger spatial scales and across more habitat types. With respect to disease vectors such as *Cx. pipiens*, the effect of small scale habitat characteristics, particularly those in suburban areas, are likely very important in the maintenance of abundance and vector potential of this species, yet remain difficult to classify and quantify. Inclusion of environmental parameters such as temperature and precipitation may also improve our understanding of spatial and temporal patterns of mosquito occurrence and seasonal phenology.

2.5 References

- Abella-Medrano, C. A., Ibáñez-Bernal, S., MacGregor-Fors, I., & Santiago-Alarcon, D. (2015). Spatiotemporal variation of mosquito diversity (Diptera: Culicidae) at places with different land-use types within a neotropical montane cloud forest matrix. *Parasites & Vectors*, 8(1), 1.
- Alencar, J., de Mello, C. F., Guimarães, A. É., Gil-Santana, H. R., dos Santos Silva, J., Santos-Mallet, J. R., & Gleiser, R. M. (2015). Culicidae community composition and temporal dynamics in Guapiaçu Ecological Reserve, Cachoeiras de Macacu, Rio de Janeiro, Brazil. *PloS ONE*, 10(3), e0122268.
- Andreadis, T. G., Anderson, J. F., & Vossbrinck, C. R. (2001). Mosquito surveillance for West Nile virus in Connecticut, 2000: isolation from *Culex pipiens*, *Cx. restuans*, *Cx. salinarius*, and *Culiseta melanura*. *Emerging Infectious Diseases*, 7(4), 670.

- Andreadis, T. G., & Wolfe, R. J. (2010). Evidence for reduction of native mosquitoes with increased expansion of invasive *Ochlerotatus japonicus japonicus* (Diptera: Culicidae) in the northeastern United States. *Journal of Medical Entomology*, 47(1), 43-52.
- Barrera, R., & Medialdea, V. (1996). Development time and resistance to starvation of mosquito larvae. *Journal of Natural History*, 30(3), 447-458.
- Becker, N., Petrić, D., Zgomba, M., Boase, C., Dahl, C. Lane, J., & Kaiser, A. (2003). Mosquitoes and their control. New York, NY: Springer. 577 pp.
- Bellini, R., Albieri, A., Balestrino, F., Carrieri, M., Porretta, D., Urbanelli, S., Calvitti, M., Moretti, R., & Maini, S. (2010). Dispersal and survival of *Aedes albopictus* (Diptera: Culicidae) males in Italian urban areas and significance for sterile insect technique application. *Journal of Medical Entomology*, 47(6), 1082-1091.
- Benelli, G., & Mehlhorn, H. (2016). Declining malaria, rising of dengue and Zika virus: insights for mosquito vector control. *Parasitology Research*, 115(5), 1747-1754.
- Bidlingmayer, W. L., & Hem, D. G. (1981). Mosquito flight paths in relation to the environment. Effect of the forest edge upon trap catches in the field. *Mosquito News*, 41, 55-59.
- Bosak, P. J., Reed, L. M., & Crans, W. J. (2001). Habitat preference of host-seeking *Coquillettidia perturbans* (Walker) in relation to birds and eastern equine encephalomyelitis virus in New Jersey. *Journal of Vector Ecology*, 26, 103-109.
- Bradshaw, M. E., & Holzapfel, C. M. (1992). Resource limitation, habitat segregation, and species interactions of British tree-hole mosquitoes in nature. *Oecologia*, 90(2), 227-237.
- Buckner, E. A., Blackmore, M. S., Golladay, S. W., & Covich, A. P. (2011). Weather and landscape factors associated with adult mosquito abundance in southwestern Georgia, USA. *Journal of Vector Ecology*, 36(2), 269-278.
- Buddle, C. M., Beguin, J., Bolduc, E., Mercado, A., Sackett, T. E., Selby, R. D., Varady-Szabo, H., & Zeran, R. M. (2005). The importance and use of taxon sampling curves for comparative biodiversity research with forest arthropod assemblages. *The Canadian Entomologist*, 137(01), 120-127.

- Burkett-Cadena, N. D., Eubanks, M. D., & Unnasch, T. R. (2008). Preference of female mosquitoes for natural and artificial resting sites. *Journal of the American Mosquito Control Association*, 24(2), 228.
- Carpenter, S. J., & LaCasse, W. J. (1955). *Mosquitoes of North America*. University of California Press. Berkeley, California. 360 pp.
- (CDC) Centers for Disease Control and Prevention. (2012). Mosquito species in which West Nile virus has been detected. Accessed October 2015. Retrieved from: <https://www.cdc.gov/westnile/vectorcontrol/index.html>
- Chase, J. M., & Knight, T. M. (2003). Drought-induced mosquito outbreaks in wetlands. *Ecology Letters*, 6(11), 1017-1024.
- Chaves, L. F., Harrington, L. C., Keogh, C. L., Nguyen, A. M., & Kitron, U. D. (2010). Blood feeding patterns of mosquitoes: random or structured? *Frontiers in Zoology*, 7(1), 1.
- Clark, C. 2005. An introduction to ordination. San Francisco State University. Accessed November 2014. Retrieved from <http://online.sfsu.edu/efc/classes/biol710/ordination/ordination.htm>
- Crans, W. J. (2004). A classification system for mosquito life cycles: life cycle types for mosquitoes of the northeastern United States. *Journal of Vector Ecology*, 29, 1-10.
- Cummins, B., Cortez, R., Foppa, I. M., Walbeck, J., & Hyman, J. M. (2012). A spatial model of mosquito host-seeking behavior. *PLoS Computational Biology*, 8(5), e1002500.
- Cupp, E. W., Klingler, K., Hassan, H. K., Viguers, L. M., & Unnasch, T. R. (2003). Transmission of eastern equine encephalomyelitis virus in central Alabama. *American Journal of Tropical Medicine and Hygiene*, 68(4), 495-500.
- Darsie Jr, R. F., & Ward, R. A. (2005). Identification and geographical distribution of the mosquitoes of North America, north of Mexico. *Journal of the American Mosquito Control Association*, 21(1), 383 pp.
- Deichmeister, J. M., & Telang, A. (2011). Abundance of West Nile virus mosquito vectors in relation to climate and landscape variables. *Journal of Vector Ecology*, 36(1), 75-85.

- Dickinson, K., & Paskewitz, S. (2012). Willingness to pay for mosquito control: How important is West Nile virus risk compared to the nuisance of mosquitoes? *Vector-borne and Zoonotic Diseases*, 12(10), 886-892.
- Döetler, S., Jahreib, K., Jhumur, U. S., & Juergens, A. (2012). Temporal variation of flower scent in *Silene otites* (Caryophyllaceae): a species with a mixed pollination system. *Botanical Journal of the Linnean Society*, 169(3), 447-460.
- Duncombe, J., Clements, A., Davis, J., Hu, W., Weinstein, P., & Ritchie, S. (2013). Spatiotemporal patterns of *Aedes aegypti* populations in Cairns, Australia: assessing drivers of dengue transmission. *Tropical Medicine & International Health*, 18(7), 839-849.
- El Adlouni, S., Beaulieu, C., Ouarda, T. B., Gosselin, P. L., & Saint-Hilaire, A. (2007). Effects of climate on West Nile Virus transmission risk used for public health decision-making in Quebec. *International Journal of Health Geographics*, 6(1), 1.
- Fader, J. E., & Juliano, S. A. (2014). Oviposition habitat selection by container-dwelling mosquitoes: responses to cues of larval and detritus abundances in the field. *Ecological Entomology*, 39(2), 245-252.
- Fauci, A. S., & Morens, D. M. (2016). Zika virus in the Americas—yet another arbovirus threat. *New England Journal of Medicine*, 374(7), 601-604.
- Ganser, C., & Wisely, S. M. (2013). Patterns of spatio-temporal distribution, abundance, and diversity in a mosquito community from the eastern Smoky Hills of Kansas. *Journal of Vector Ecology*, 38(2), 229-236.
- Golding, N., Nunn, M. A., & Purse, B. V. (2015). Identifying biotic interactions which drive the spatial distribution of a mosquito community. *Parasites & Vectors*, 8(1), 1-10.
- Gonsalves, L., Lamb, S., Webb, C., Law, B., & Monamy, V. (2013). Do mosquitoes influence bat activity in coastal habitats? *Wildlife Research*, 40(1), 10-24.
- Gubler, D. J. (1998). Resurgent vector-borne diseases as a global health problem. *Emerging Infectious Diseases*, 4(3), 442.
- Guedes, M. L. P., & Navarro-Silva, M. A. (2014). Mosquito community composition in dynamic landscapes from the Atlantic Forest biome (Diptera, Culicidae). *Revista Brasileira de Entomologia*, 58(1), 88-94.

- Howard, J. J., Emord, D. E., & Morris, C. D. (1983). Epizootiology of Eastern Equine Encephalomyelitis Virus in Upstate New York, USA V. Habitat preference of host-seeking mosquitoes (Diptera: Culicidae). *Journal of Medical Entomology*, 20(1), 62-69.
- Haddow, A. D., Gerhardt, R. R., Jones, C. J., & Odoi, A. (2009). The mosquitoes of eastern Tennessee: studies on abundance, habitat preferences, and host-seeking behaviors. *Journal of Vector Ecology*, 34(1), 70-80.
- Halasa, Y. A., Shepard, D. S., Fonseca, D. M., Farajollahi, A., Healy, S., Gaugler, R., Bartlett-Healy, K., Strickman, D.A. & Clark, G. G. (2014). Quantifying the impact of mosquitoes on quality of life and enjoyment of yard and porch activities in New Jersey. *PloS one*, 9(3), e89221.
- Holland, S.M. 2008. Non-Metric Multidimensional Scaling (MDS). University of Georgia. Retrieved from <http://strata.uga.edu/software/pdf/mdsTutorial.pdf>
- Johnson, M. F., Gómez, A., & Pinedo-Vasquez, M. (2008). Land use and mosquito diversity in the Peruvian Amazon. *Journal of Medical Entomology*, 45(6), 1023-1030.
- Johnson, B. J., Munafo, K., Shappell, L., Tsipoura, N., Robson, M., Ehrenfeld, J., & Sukhdeo, M. V. (2012). The roles of mosquito and bird communities on the prevalence of West Nile virus in urban wetland and residential habitats. *Urban Ecosystems*, 15(3), 513-531.
- Juliano, S. A., & Philip Lounibos, L. (2005). Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecology Letters*, 8(5), 558-574.
- Juliano, S. A. (2009). Species interactions among larval mosquitoes: context dependence across habitat gradients. *Annual Review of Entomology*, 54, 37.
- Junglen, S., Kurth, A., Kuehl, H., Quan, P. L., Ellerbrok, H., Pauli, G., Nitsche, A., Nunn, C., Rich, S. M., Lipkin, W. I., Briese, T., & Leenderts, F. H. (2009). Examining landscape factors influencing relative distribution of mosquito genera and frequency of virus infection. *Ecohealth*, 6(2), 239-249.
- Kilpatrick, A. M., Kramer, L. D., Jones, M. J., Marra, P. P., & Daszak, P. (2006). West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. *PLoS Biology*, 4(4), e82.

- Kling, L. J., Juliano, S. A., & Yee, D. A. (2007). Larval mosquito communities in discarded vehicle tires in a forested and unforested site: detritus type, amount, and water nutrient differences. *Journal of Vector Ecology: Journal of the Society for Vector Ecology*, 32(2), 207.
- Lambrechts, L., Scott, T. W., & Gubler, D. J. (2010). Consequences of the expanding global distribution of *Aedes albopictus* for dengue virus transmission. *PLoS Neglected Tropical Diseases*, 4(5), e646.
- Lysyk, T. J. (2010). Species abundance and seasonal activity of mosquitoes on cattle facilities in southern Alberta, Canada. *Journal of Medical Entomology*, 47(1), 32-42.
- MacArthur, R. (1960). On the relative abundance of species. *American Naturalist*, 25-36.
- MacKenzie, D. I., Bailey, L. L., & Nichols, J. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, 73(3), 546-555.
- McElhinny, C., Gibbons, P., Brack, C., & Bauhus, J. (2005). Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management*, 218(1), 1-24.
- Medlock, J. M., Hansford, K. M., Schaffner, F., Versteirt, V., Hendrickx, G., Zeller, H., & Bortel, W. V. (2012). A review of the invasive mosquitoes in Europe: ecology, public health risks, and control options. *Vector-borne and zoonotic diseases*, 12(6), 435-447.
- Medlock, J. M., & Vaux, A. G. (2015). Seasonal dynamics and habitat specificity of mosquitoes in an English wetland: implications for UK wetland management and restoration. *Journal of Vector Ecology*, 40(1), 90-106.
- Meide, L., Xuezhong, W., Tongyan, Z., Zhunwei, D., Yande, D., & Baolin, L. (2008). Analysis of the relationship between density and dominance of *Anopheles minimus* (Diptera: Culicidae) with environmental parameters in southern Yunnan Province, Peoples Republic of China. *Journal of Medical Entomology*, 45(6), 1007-1010.

- Molyneux, D. H., Ostfeld, R. S., Bernstein, A., & Chivian, E. (2008). *Sustaining life: how human health depends on biodiversity*, (Chapter 7) Ecosystem disturbance, biodiversity loss, and human infectious disease. Oxford University Press. 568 pp.
- Nasci, R. S., Moore, C. G., Biggerstaff, B. J., Panella, N. A., Liu, H. Q., Karabatsos, N., Davis, B.S. & Brannon, E. S. (2000). La Crosse encephalitis virus habitat associations in Nicholas County, West Virginia. *Journal of Medical Entomology*, 37(4), 559-570.
- Norris, D. E. (2004). Mosquito-borne diseases as a consequence of land use change. *EcoHealth*, 1(1), 19-24.
- Oksanen, J. 2015. Vegan: an introduction to ordination. University of Oulu. Accessed May 2016. Retrieved from: <http://cran.r-project.org/web/packages/vegan/vignettes/intro-vegan.pdf>
- Parks Canada. (2009, April 15). The St. Lawrence lowlands. Accessed June 2016. Retrieved from <http://www.pc.gc.ca/eng/docs/v-g/nation/nation75.aspx>
- Pecoraro, H. L., Day, H. L., Reineke, R., Stevens, N., Withey, J. C., Marzluff, J. M., & Meschke, J. S. (2007). Climatic and landscape correlates for potential West Nile virus mosquito vectors in the Seattle region. *Journal of Vector Ecology*, 32(1), 22-28.
- Poppe, J. L., Schmitz, H. J., Callegari-Jacques, S. M., & Valente, V. L. S. (2015). Environmental determinants on the assemblage structure of drosophilidae flies in a temperate-subtropical region. *Neotropical Entomology*, 44(2), 140-152.
- Roche, B., Léger, L., L'Ambert, G., Lacour, G., Foussadier, R., Besnard, G., Barré-Cardi, F.S. & Fontenille, D. (2015). The spread of *Aedes albopictus* in metropolitan France: Contribution of environmental drivers and human activities and predictions for a near future. *PloS ONE*, 10(5), e0125600.
- Rochlin, I., Harding, K., Ginsberg, H. S., & Campbell, S. R. (2008). Comparative analysis of distribution and abundance of West Nile and eastern equine encephalomyelitis virus vectors in Suffolk County, New York, using human population density and land use/cover data. *Journal of Medical Entomology*, 45(3), 563-571.

- Rochlin, I., Ninivaggi, D. V., Hutchinson, M. L., & Farajollahi, A. (2013). Climate change and range expansion of the Asian tiger mosquito (*Aedes albopictus*) in Northeastern USA: implications for public health practitioners. *PloS ONE*, 8(4), e60874.
- Rossi, V. 2010. Ordination methods for analyzing ecological data. Université Antilles-Guyane. Accessed November 2014. Retrieved from <http://vrossi.free.fr/DONNEES/ordination.pdf>
- Rueda, L. M. (2008). Global diversity of mosquitoes (Insecta: Diptera: Culicidae) in freshwater. *Hydrobiologia*, 595(1), 477-487.
- Rydzanicz, K., & Lonc, E. (2003). Species composition and seasonal dynamics of mosquito larvae in the Wroclaw, Poland area. *Journal of Vector Ecology*, 28, 255-266.
- Schowalter, T. D. (2011). *Insect ecology: an ecosystem approach (3rd ed.)*. Academic Press. San Diego, California, USA. 633 pp.
- Sérandour, J., Willison, J., Thuiller, W., Ravanel, P., Lempérière, G., & Raveton, M. (2010). Environmental drivers for *Coquilleltidia* mosquito habitat selection: a method to highlight key field factors. *Hydrobiologia*, 652(1), 377-388.
- Service, M. W. (1980). Effects of wind on the behaviour and distribution of mosquitoes and blackflies. *International Journal of Biometeorology*, 24, 347-353.
- Shone, S. M., Ferrao, P. N., Lesser, C. R., Norris, D. E., & Glass, G. E. (2001). Analysis of mosquito vector species abundances in Maryland using geographic information systems. *Annals of the New York Academy of Sciences*, 951(1), 364-368.
- Silver, J. B. (2008). *Mosquito ecology: field sampling methods (3rd ed.)*. Springer Science & Business Media. New York, NY. 1477 pp.
- Singer, R. B. (2001). Pollination biology of *Hebenaria parviflora* (Orchidaceae: Habenariinae) in southeastern Brazil. *Darwiniana*, 201-207.
- Smith, D. L., Dushoff, J., & McKenzie, F. E. (2004). The risk of a mosquito-borne infection in a heterogeneous environment. *PLoS Biology*, 2(11), e368.
- Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist*, 152(4), 510-529.

- Steiger, D. M., Johnson, P., Hilbert, D. W., Ritchie, S., Jones, D., & Laurance, S. G. (2012). Effects of landscape disturbance on mosquito community composition in tropical Australia. *Journal of Vector Ecology*, 37(1), 69-76.
- Stein, M., Santana, M., Galindo, L. M., Etchepare, E., Willener, J. A., & Almirón, W. R. (2016). Culicidae (Diptera) community structure, spatial and temporal distribution in three environments of the province of Chaco, Argentina. *Acta Tropica*, 156, 57-67.
- Stoddard, S. T., Morrison, A. C., Vazquez-Prokopec, G. M., Soldan, V. P., Kochel, T. J., Kitron, U., Elder, J.P., & Scott, T. W. (2009). The role of human movement in the transmission of vector-borne pathogens. *PLoS Neglected Tropical Diseases*, 3(7), e481.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), 79-92.
- Thielman, A. C., & Hunter, F. F. (2007). *A photographic key to adult female mosquito species of Canada (Diptera: Culicidae)*. Canadian Journal of Arthropod Identification, 4, 1-117.
- Trojan, P. (1992). Fauna structure analysis. *Memorabilia Zoologica*, 47, 1-120.
- Turell, M. J., Dohm, D. J., Sardelis, M. R., O'guinn, M. L., Andreadis, T. G., & Blow, J. A. (2005). An update on the potential of North American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. *Journal of Medical Entomology*, 42(1), 57-62.
- Whittaker, R. H. (1965). Dominance and diversity in land plant communities. *Science*, 147(3655), 250-260.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21(2), 213-251.

- Wilkerson, R. C., Linton, Y. M., Fonseca, D. M., Schultz, T. R., Price, D. C., & Strickman, D. A. (2015). Making mosquito taxonomy useful: a stable classification of tribe Aedini that balances utility with current knowledge of evolutionary relationships. *PLoS ONE*, 10(7), e0133602.
- Wood, D. M., Dang, P. T., & Ellis, R. A. (1979). The insects and arachnids of Canada. Part 6. The mosquitoes of Canada. Diptera: Culicidae. Canadian Government Publishing Centre. Hull, Quebec. 390 pp.
- Yan, Z. C., & Zhong, H. (2005). Comparison of adult mosquito community structure on various habitats. *Insect Science*, 12(3), 193-197.
- Yee, D. A. (2008). Tires as habitats for mosquitoes: a review of studies within the eastern United States. *Journal of Medical Entomology*, 45(4), 581-593.
- Zhong, H. E., Yan, Z., Jones, F., & Brock, C. (2003). Ecological analysis of mosquito light trap collections from West Central Florida. *Environmental Entomology*, 32(4), 807-815.

2.6 Tables and Figures

Table 2.1. Total numbers of mosquito species collected in 2014 and 2015 from Montreal, Québec, Canada.

Species		Year	
		2014	2015
<i>Aedes</i>			
	<i>abseratus</i> (Felt & Young)	0	4
	<i>canadensis</i> (Theobald)	15,738	14,400
	<i>cinereus</i> (Meigen)	1,103	2,583
	<i>communis</i> (De Geer)	4	897
	<i>diantaeus</i> (Howard, Dyar, & Knab)	268	423
	<i>dorsalis</i> (Meigen)	2	44
	<i>eudes</i> (Howard, Dyar, & Knab)	6	194
	<i>excrucians</i> (Walker)	727	538
	<i>fitchii</i> (Felt & Young)	274	528
	<i>implicatus</i> (Vockeroth)	0	17
	<i>intrudens</i> (Dyar)	0	48
	<i>japonicus</i> (Theobald)	18	40
	<i>pionips</i> (Dyar)	6	42
	<i>provocans</i> (Walker)	41	6,533
	<i>punctor</i> (Kirby)	13	2,075
	<i>rempeli</i> (Vockeroth)	0	5
	<i>sticticus</i> (Meigen)	9	24
	<i>stimulans</i> (Walker)	2,317	6,003
	<i>triseriatus</i> (Say)	366	330
	<i>trivittatus</i> (Coquillett)	1,289	15,646
	<i>vexans</i> (Meigen)	10,569	62,169
<i>Anopheles</i>			
	<i>earlei</i> (Vargas)	0	1
	<i>punctipennis</i> (Say)	92	304
	<i>quadrimaculatus</i> (Say)	4	8
	<i>walkeri</i> (Theobald)	85	188
<i>Coquillettidia</i>			
	<i>perturbans</i> (Walker)	8,897	24,588
<i>Culex</i>			
	<i>pipiens</i> (Linnaeus)	315	1,169
	<i>restuans</i> (Theobald)	9	21
<i>Culiseta</i>			
	<i>melanura</i> (Coquillett)	1	19
	<i>minnesotae</i> (Barr)	0	42
	<i>morsitans</i> (Theobald)	67	93
<i>Orthopodomyia</i>			
	<i>alba</i> (Baker)	1	0
<i>Psorophora</i>			
	<i>ciliata</i> (Fabricius)	1	61
	<i>ferox</i> (Humboldt)	32	652
<i>Uranotaenia</i>			
	<i>sapphirina</i> (Osten Sacken)	269	989
	Unidentifiable	920	486
Total no. Individuals		43,443	141,164

Table 2.2. PERMANOVA post-hoc analysis habitat comparisons for 2014 & 2015. Significant P-values in boldface.

Between Habitat Interaction	Adjusted <i>P</i> -value
2014	
Suburb vs Field	0.015
Suburb vs. Forest	0.030
Field vs. Forest	0.030
2015	
Suburb vs. Field	0.075
Suburb vs. Forest	0.015
Field vs. Forest	0.015

Table 2.3. ANOVA results for abundance and richness across all sites for both 2014 & 2015. Significant P-values in boldface.

Site Interaction	Abundance		Observed Richness	
	2014	2015	2014	2015
BRM-BDU	0.0140	0.0496	0.0395	0.0372
FIELD-BDU	0.0016	0.0000	0.5574	0.1413
HEM-BDU	0.0111	0.0105	0.0938	0.0031
SADB-BDU	0.9998	0.9290	0.9958	0.4980
SM-BDU	0.0132	0.0592	0.1970	0.0402
FIELD-BRM	0.9361	0.0173	0.4130	0.9103
HEM-BRM	0.9999	0.9535	0.9958	0.7556
SADB-BRM	0.0220	0.2406	0.0938	0.5843
SM-BRM	0.9998	0.9993	0.8427	0.9997
HEM-FIELD	0.9668	0.0885	0.7086	0.2057
SADB-FIELD	0.0025	0.0002	0.8427	0.9700
SM-FIELD	0.8055	0.0051	0.9537	0.9669
SADB-HEM	0.0174	0.0589	0.2089	0.0830
SM-HEM	0.9987	0.8163	0.9846	0.5414
SM-SADB	0.0214	0.3053	0.4130	0.6813

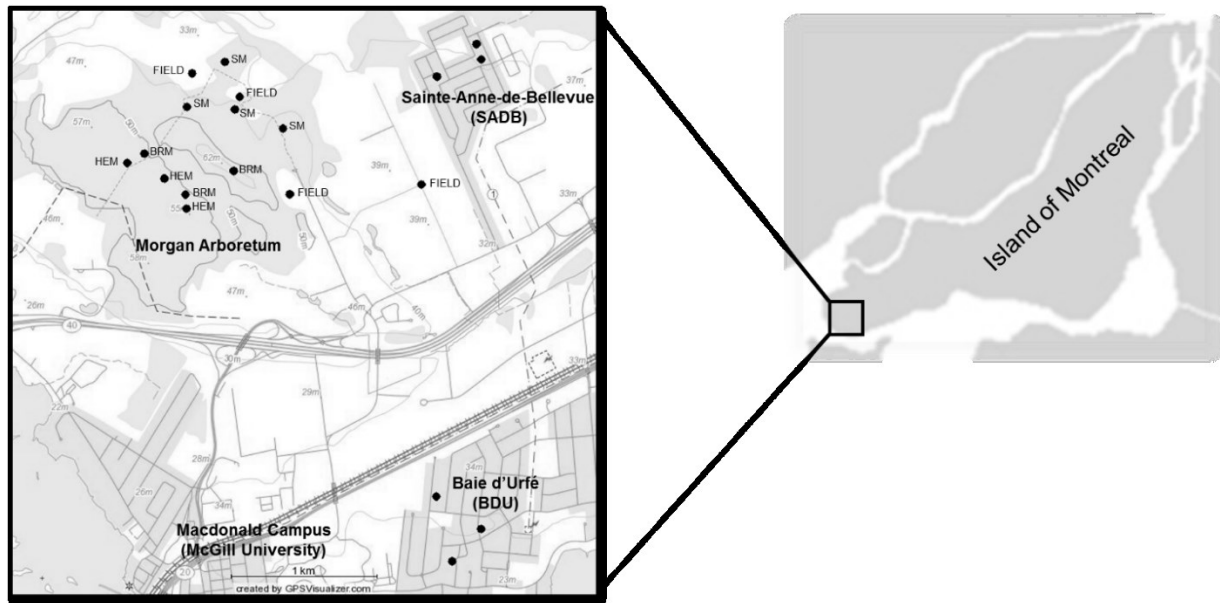


Figure 2.1. Map of the study area located on the western tip of the island of Montréal, Canada. Insert shows sampling locations as black dots. Abbreviations: suburban locations (BDU=Baie d’Urfé, SADB=Sainte-Anne-de-Bellevue) Forested (SM=Sugar Maple, BRM=Beech-Red Maple, HEM=Eastern Hemlock) and Field.

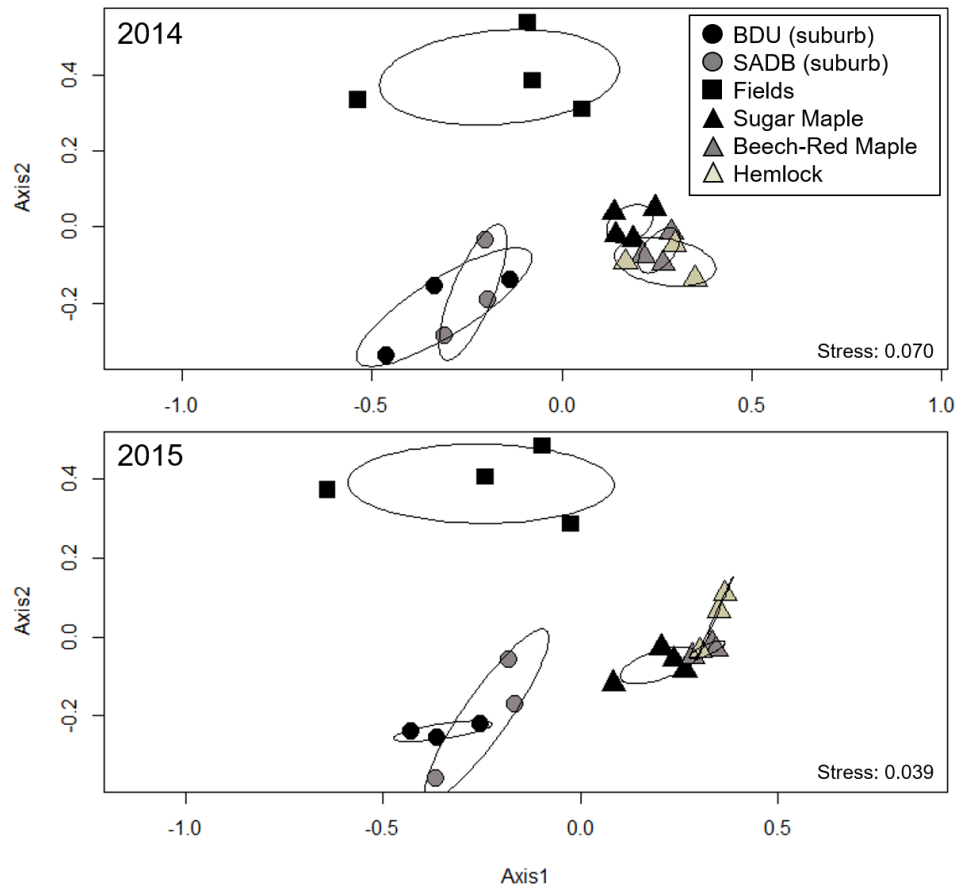


Figure 2.2. NMDS ordinations for both 2014 (top) and 2015 (bottom). Ellipses represent the SE about the mean for each site. Stress values: 2014 (0.070), 2015 (0.039).

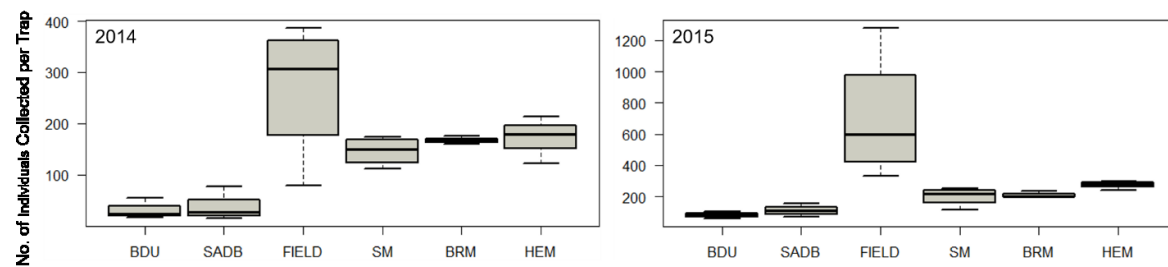


Figure 2.3. Mean number of individuals collected per trap for all six sites in 2014 (left) & 2015 (right). Boxes show the upper and lower quartiles, the horizontal line within the box shows the median value and the whiskers show the maximum and minimum observed values.

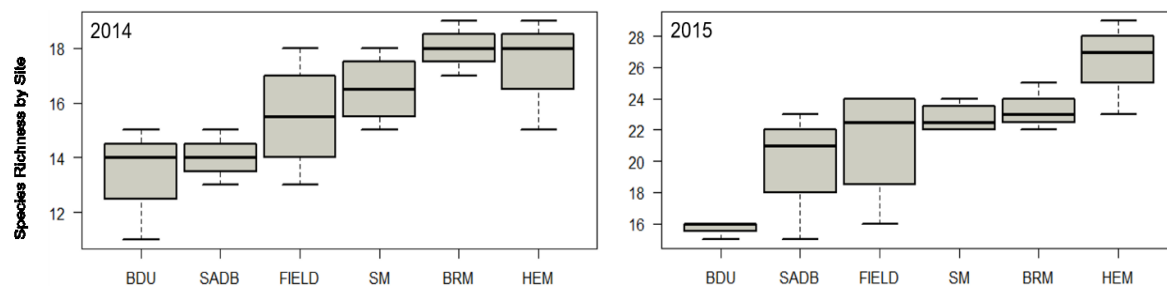


Figure 2.4. Species richness for all six sites in both 2014 (Left) & 2015 (Right). Boxes show the upper and lower quartiles, the horizontal line within the box shows the median value and the whiskers show the maximum and minimum observed values.

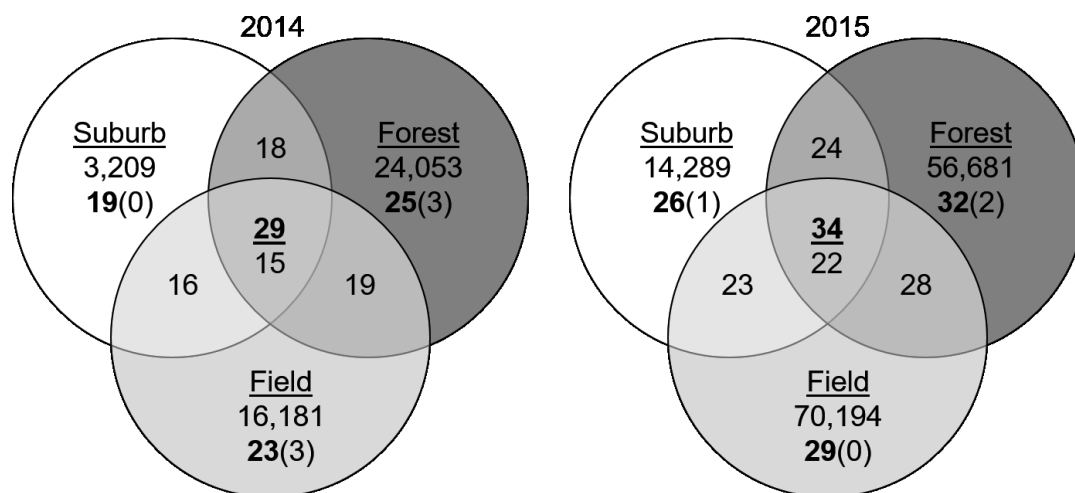


Figure 2.5. Total abundance, species richness and shared species for each habitat type for 2014 & 2015. Total number of mosquitoes collected appears first, numbers in bold indicate total number of species collected and numbers in parentheses show the number of unique species. Numbers in overlapping areas indicate the number of shared species. Total species collected (bold and underlined) as well as the total number of shared species for each year appear in the centre of each diagram.

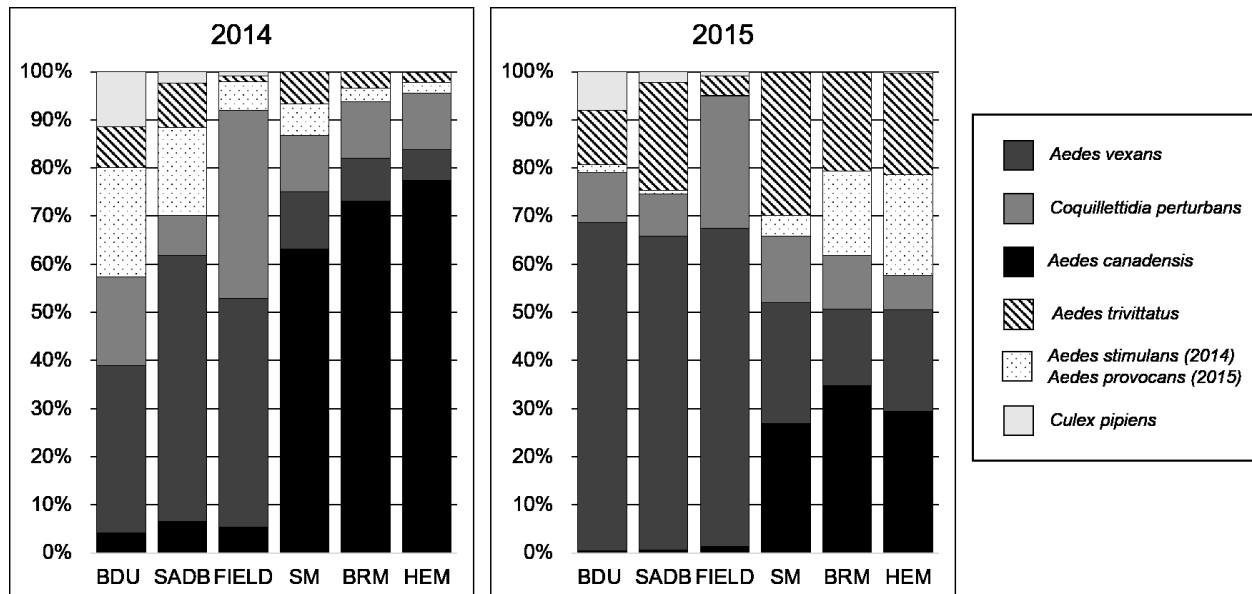
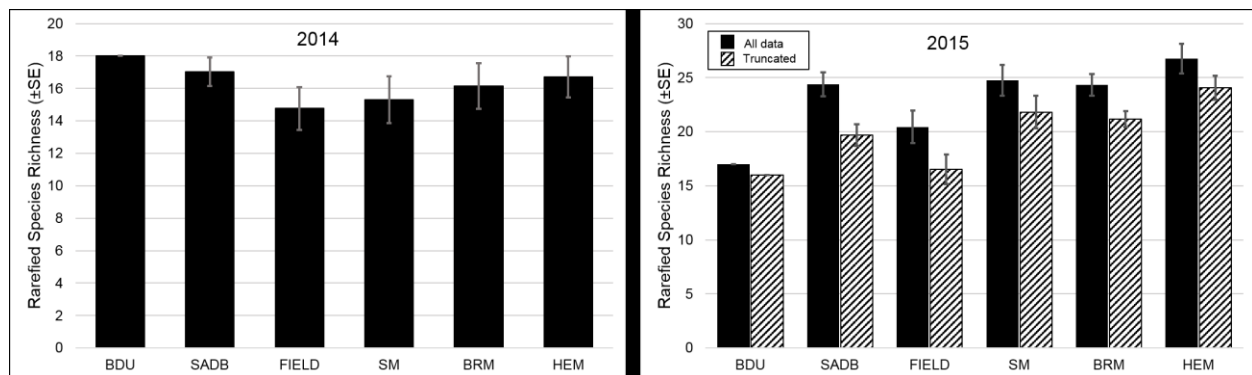


Figure 2.6. Stacked bargraphs depicting relative abundance of the five most abundant species collected from each of the six sites in both 2014 (left) and 2015 (right) Note: Four of these species were ranked highest in both years and the fifth position was held by different species in 2014 & 2015, these being *Aedes stimulans* and *Aedes provocans*, respectively. *Culex pipiens* is included due to WNV vector potential.



Appendix 2.1. Rarefied species richness for 2014, 2015 and truncated 2015 data sets

2.7 Connecting Statement

The overarching theme of this thesis is to determine how the abundance and diversity of mosquito populations and communities are shaped by habitat and environmental variables on the west island of Montreal. Chapter 2 focused specifically on the effect of habitat in determining the community structure of mosquitoes and how these habitats affect specific patterns of abundance, species richness, species sharing and the relative abundance of dominant species

Chapter 2 provided information on how mosquitoes are related to their physical environment. Although it highlighted data from both sampling seasons, it only examined minor aspects of inter-annual changes in community structure. Chapter 3 provides an in-depth look at the temporal aspects of mosquito community and population level changes by analysing inter-annual community structure and phenology.

Chapter 3: The effect of temperature and precipitation on the phenology and abundance of mosquito (Culicidae) communities in suburban, field and forested habitats in Montreal (Canada)

3.1 Introduction

Mosquitoes (Diptera: Culicidae) remain a focal point of entomology research, due to their medical and economic importance around the world (Becker et al. 2003, Williams, 2009). They are best known for their role as nuisance pests or as disease vectors and are associated with debilitating and often life threatening diseases such as malaria, Dengue fever, filariasis and others (Tolle, 2009; Gubler, 2010; Bhatt et al., 2013). Approximately 17% of all infectious diseases are vector-borne, many of which are spread by mosquitoes. It is estimated that these diseases put billions of people at risk and result in nearly 1 million deaths annually (WHO, 2016). Within the North American context, several arbovirus infections have been established for many years, including West Nile virus, Eastern Equine encephalitis, and LaCross virus (Calisher, 1994; Hayes & Gubler, 2006; Haddow, 2009; CDC, 2016), and more recently, Zika virus and Chikungunya virus (loos et al., 2014; Weaver, 2014; Petersen et al., 2016). The biology and phenology of mosquitoes of many different species has been studied extensively in an effort to better predict when and how outbreaks of mosquitoes and their associated diseases will occur and how to better manage mosquito populations.

Studies that attempt to model mosquito occurrence and phenological patterns tend to focus on primary vector species. These models often incorporate data collected from field surveillance studies and generally incorporate meteorological or environmental variables as explanatory conditions determining the growth rates, nuisance potential and vector competence of these species (Jacups et al., 2015; Ewing et al., 2016). Studies such as these become increasingly more important in light of global climate change, since increases in global temperatures as well modifying patterns of precipitation affect mosquitoes (McMichael et al., 2006; Gould & Higgs, 2009).

With high fecundity and rapid development, mosquitoes are subject to species level fluctuations in population size and seasonal abundance, producing distinct community structure. Communities change as their complement of associated species changes and thus it is important to know the phenology and abundance of all species which comprise this community. From year to year, populations and the resulting community structure can vary substantially and are affected by a complex array of environmental factors (Fontenille et al., 1997; Schäfer et al., 2008; Ganser & Wisely, 2013). However, temperature and precipitation seem to be the most commonly used variables to explain fluctuations in mosquito populations, which aligns with what is known about mosquito biology. For example, temperature is important in the timing of egg hatch (Lysyk, 2010), the growth and development of larvae (Clements, 1992; Paaajmans et al., 2010; Chuang et al., 2011), and the longevity, biting frequency and activity of adults (Becker, 2008; Ciota et al., 2014; Shand et al., 2016). Precipitation plays a principle role in the quality and availability of breeding sites (Gong et al., 2011), which in turn can result in larger populations of mosquitoes and also influence the number of generations in a given year, an important variable in nuisance and vector cycles as well as in describing the local community structure (Horsfall et al., 1973; Bicout & Sabatier, 2004; Hu et al., 2006; Ponçon et al., 2007).

The primary objective of this research was to quantify temporal variation in mosquito community structure by analysing community composition and relative dominance across different habitat types over a two-year period of mosquitoes collected on the western portion of the island of Montreal, Quebec, Canada. A second objective was to describe the patterns of annual phenology of dominant species and link this to the timing of peak emergence at the community and species levels and to determine the effects of temperature and precipitation over a biologically plausible temporal scale.

3.2 Methods

3.2.1 Study site

Sample sites were located on the western tip of the island of Montreal in Québec, Canada (45° 31' N, 73° 34' W). This area is characterized by multiple suburban

communities with a patchwork of natural areas and farmlands. The region is found within the mixedwood plains ecozone, a temperate region with a relatively mild climate compared to other parts of Canada (Canadian Climate Impacts and Adaptation Research Network, 2002). Climate is moderated to some extent by proximity to the St. Lawrence river and other large water bodies, with average temperatures ranging from -5°C in winter to 17°C in summer (The Canadian Biodiversity Website).

Twenty sampling locations were chosen across different habitat types (Fig 3.1). These were divided into three broad categories defined as “suburban”, characterized by single family housing with parks, trees, and adjacent green spaces, “forest”, comprised of large overstory trees, and “fields”, open areas lacking tree cover and comprised of low growing herbaceous vegetation or agricultural crops. At least three replicate locations were sampled for each habitat type. Three locations were sampled in each of two suburban municipalities (Baie d’Urfé (BDU) and Sainte-Anne-de-Bellevue (SADB)). Forested habitats were located within the Morgan Arboretum, a 245 ha forested property located within the town of Sainte-Anne-de-Bellevue. Three forest types, distinguished by dominant overstory tree species composition (Sugar Maple (*Acer saccharum*) (SM), American Beech-Red Maple (*Fagus grandifolia/Acer rubrum*) (BRM) and Eastern Hemlock (*Tsuga canadensis*) (HEM)) were studied, each receiving three traps, with the exception of Sugar Maple with four. Four field locations were chosen, each receiving a single trap.

3.2.2 Sample collection and specimen processing

Mosquitoes were sampled weekly from 25 June to 1 October in 2014, and from 19 April to 14 October, 2015 for a total of 15 and 25 sampling weeks per year, respectively. Traps were serviced once a week for a total of 300 and 500 trap collections for 2014 and 2015, respectively. Traps used were All-weather LED EVS traps (Bioquip Products, Inc®, Rancho Dominguez, CA) baited with 1.5 kg of dry ice and suspended 1.5 m above the ground. Traps were deployed early afternoon and remained open for 24 h to sample in all activity periods (i.e., daylight, crepuscular, night). After 24 h, trap bags were removed and specimens placed into the freezer for later identification.

Identification was done with the use of keys to morphological characters (Wood et al., 1979, Darsie & Ward, 2005; Thielman & Hunter, 2007). All adult female specimens were identified to species and counted in the samples from each collected trap. If a specimen was too damaged to identify to species, it was counted but left as unknown. The naming and abbreviations used herein for all genera follow the classification outlined by Wilkerson et al. (2015). Voucher specimens of all species are deposited at the Lyman Entomological Museum, McGill University (Ste-Anne-de-Bellevue, Québec, Canada).

3.2.3 Environmental data

Daily weather data, including mean daily temperature and total daily precipitation, were obtained from the Government of Canada Historical Climate database (Environment Canada, 2016). Data were obtained from the Sainte-Anne-de-Bellevue station (45° 25' N, 73° 56' W) World Meteorological Organization (WMO) identifier – 71377. This station is centrally located between all sample sites with the furthest site being located less than 3 km away (Fig. 3.1). Mean weekly temperature (°C) and total weekly precipitation (mm) were generated for every week (Sunday-Saturday) of sampling and at least four weeks before the start of sample collection. Inter-annual differences of these variables were assessed using ANOVA (adonis; vegan library version 2.2-1; Oksanen, 2015; R version 3.1.3). Weeks were numbered based on the numbers provided at (week-number.net). Weather data were compiled each week beginning at the end of March (week 14) until the end of the sampling period, generally in the second week of October (week 40-42). The sampling period for 2014 comprised week 26 to 40 inclusive, and in 2015 from week 18 to 42, inclusive for a total of 15 and 25 sampling periods, respectively.

3.2.4 Data analyses

Variation in community structure between years and with habitat was assessed using NMDS ordination (metaMDS; vegan library version 2.2-1; Oksanen, 2015; R version 3.1.3). All computational analyses were performed in R version 3.1.3 unless otherwise noted (R Development Core Team, 2015). Site data were pooled by year and habitat

type. Abundance data were double root transformed to remove the effect of very abundant species for analysis. The significance of the interaction between year and habitat on mosquito community structure was assessed using permutational multivariate analysis of variance (PERMANOVA) using distance matrices. Bonferroni Post Hoc Multiple Comparison Test was used to perform a pairwise comparison across all habitats and years. This allows a direct comparison of the dissimilarity between the years, habitat type, and the nature of the differences experienced in each year by habitat.

Within year and between year changes in community structure were analysed by interpreting the populations of dominant species. The three most dominant species in both years, and those considered for analysis were; *Aedes vexans* (Meigen) a well-known nuisance species in Canada (Wood et al., 1979), *Aedes canadensis* (Theobald) and *Coquilleltidia perturbans* (Walker). The populations of these along with the medically important species, *Culex pipiens* (L.) were compared to all other species collected. Dominant species typically had >10% representation in the community. Relative proportions were generated by (number of individuals of a given species in week “x” / total number of mosquitoes in week “x”)*100.

The relationship of mosquito abundance with environmental variables was interpreted using linear regression analysis (*lm* function; R version 3.1.3) fitting dependant variable (abundance) against the independent variables (mean weekly temperature, total weekly precipitation, synergistic effect of both). Synergistic effect was analysed since these variables are considered largely interdependent (Shand et al., 2016). The strength of the relationship was examined at different time lag intervals ranging from 0 weeks (week of collection) to 4 weeks prior to sample collection. The period of four weeks is based on the average developmental rate in temperate regions, generally 1-3 weeks depending on the range of conditions encountered (Carpenter & Lacasse, 1955; EPA, 2016). Research has also shown that these variables have a diminished effect beyond four weeks (Shand et al., 2016). Lag effect models were generated for total mosquito

abundance in both 2014 and 2015 as well as for the four focal species collected in each year (*Ae. vexans*, *Ae. canadensis*, *Cq. perturbans* and *Cx. pipiens*).

3.3 Results

3.3.1 General results

A total of 184,607 mosquitoes was collected between 2014 and 2015. Yearly totals were 43,443 and 141,164, respectively. These represented 35 species in 8 genera. Three species (*Ae. vexans* (Meigen), *Cq. perturbans* (Walker), and *Ae. canadensis* (Theobald)) comprised 80% and 71% of the total number of mosquitoes collected across both sampling seasons, respectively.

Average temperatures recorded for 2014 and 2015 were 15.5°C and 15.6°C, respectively, with no significant difference between the two years ($F=0.004$, $P=0.948$). Total precipitation in 2014 was 628.8 mm and 593.2 mm in 2015 which was not significantly different between years ($F=0.327$, $P=0.57$).

3.3.2 Community structure

NMDS ordination shows that inter-annual community structure was dissimilar across most different habitat types (Fig. 3.2). PERMANOVA reveals year, habitat, and the nature of the variation in each habitat across both years are all significant. Their respective P-values are 0.001, 0.001, and 0.023 (Table 3.1). Pair-wise comparison reveals that habitat types showed significant differences in community structure regardless of year. Inter-annual comparisons between like habitats were significant with the exception of suburban habitat from 2014 vs. 2015 ($P=0.060$).

3.3.3 Species dominance

Despite unequal sampling effort and different number of mosquitoes collected between the years, some patterns are similar across years (Fig. 3.3). In 2014, sampling began in week 26 (June wk3), a period which focal species were already present in the adult stage. The extended sampling season in 2015 revealed that the first major appearance

of these species occurred in week 25, suggesting that first emergence of these species was captured in 2014. Seasonal community composition varied across the entire season in both years and dominant species turnover was evident (Fig. 3.3). In 2014 (Fig. 3.3a), *Ae. canadensis* was dominant in weeks 26-34, with the exception of weeks 30 and 33. *Cq. perturbans* had higher abundance early with greatest numbers collected from week 27-33, being dominant only in week 30. *Ae. vexans* became the dominant species following week 33 and remained so for the entire season with the exception of week 34. *Cx. pipiens* appeared at week 30 and was present in low numbers until the end of collection.

The early weeks of 2015 were marked by a lack of focal species, with 100% dominance by “others” for the first three weeks (18-20) followed by a steady climb in the abundance of our focal species over the next three weeks (22-24) (Fig 3.3b). Early season dominance was again attributed to *Ae. canadensis* and *Cq. perturbans*. Following this, *Ae. vexans* again became dominant until the end of the season. Similar to 2014, *Cx. pipiens* appeared in week 30 and its relative dominance increased into the later weeks of the year, with greatest relative proportions collected in weeks 41 & 42.

3.3.4 Phenology

The greatest number of mosquitoes collected in 2014 was in week 27 (July wk1) with 11,455 individuals (Fig. 3.4a). In 2015, two peaks were observed, one in week 28 (July wk2) with a total of 15,538 individuals, and a second, larger peak in week 33 (August wk2) which had a total abundance of 23, 275 individuals (Fig. 3.4b). The major peak in 2014 and the first peak in 2015 occurred on similar dates.

3.3.5 Species-level phenology

In 2014, all species experienced peaks at week 27 with the exception of *Cx. pipiens* (Fig. 3.5). *Cq. perturbans* had two peaks in 2014, with the second occurring in weeks 29-30. In 2015 *Ae. canadensis* and *Cq. perturbans* peaked at a similar time to the previous year at week 28. *Ae. vexans* peaked later in the season compared to 2014, reaching peak abundance in week 32. *Cx. pipiens* was consistent with peak abundance

in 2014, occurring again in week 32. In both years, most species experienced rapid drop off in numbers following their peak (Fig. 3.5). Conversely, *Cx. pipiens* numbers remained comparatively high until week 40.

3.3.6 Environmental variables and lag effects

All significant interactions from model fitting with total mosquito abundance and environmental variables were positive, suggesting that as either variable increased, there was a corresponding increase in mosquito abundance (Table 3.2). The only consistent negative relationship observed in both years was with weekly precipitation at lag 0. Negative relationships suggest an inverse correlation between the two variables (Chuang et al., 2011). In 2014, the strongest relationship between abundance and temperature was found at lag 0 ($R^2=0.3549$; $P=0.011$) and precipitation at lag interval 3 ($R^2=0.257$; $p=0.031$). The combined effect of temperature and precipitation showed the greatest correlation at lag 0 but was non-significant ($R^2=0.2687$; $p=0.060$). In 2015, responses to temperature were greatest at lag 1 ($R^2=0.2837$; $p=0.003$), yet lag 0 and lag 2 also produced significant interactions. Precipitation effect was greatest at 2 weeks lag ($R^2=0.1931$; $p=0.016$) and similarly, combined variable effects were also greatest at a lag of 2 weeks ($R^2=0.2927$; $p=.0008$). 2014 and 2015 do show some similarities, but abundance varied annually as a function of environmental parameters. In both years, temperature overall showed greater influence closer to the date of sampling and precipitation was generally most significant several weeks before sampling, as would be consistent with the timing of reproduction. In 2014, the strongest explanatory variable of abundance was temperature, and in 2015 it was the combined effect of temperature and precipitation.

3.3.7 Environmental variables and lag effects-species level

Most species showed a significant interaction and positive increase in abundance in response to temperature occurring near the week of collection (Table 3.3), exceptions being *Cx. pipiens* in 2014 and *Cq. perturbans* in 2015, with no significant interaction. This relationship can vary annually as shown by *Ae. Canadensis*, which in 2014 had its

greatest correlation to a lag of 4 weeks, and in 2015 at lag 0. In general, most interactions observed with temperature occurred at short time intervals.

Species abundance correlates to precipitation generally over longer time intervals. Only *Ae. canadensis* and *Ae. vexans* had a positive and significant response to precipitation in 2014 at three and four weeks lag, respectively (Table 3.3). In 2015, only *Ae. vexans* had a significant positive response, which occurred at two weeks lag. Both *Cq. perturbans* and *Cx. pipiens* showed no significant interaction with precipitation in either year and all correlations were weak or negative.

In 2014, *Ae. canadensis* and *Ae. vexans* showed significant response to the combined variables. Despite this, the greatest correlation for *Ae. vexans*, *Cq. perturbans* and *Cx. pipiens* occurred at lag 0, or during the week of collection (Table 3.3). In 2015, *Cq. perturbans* again showed no significant interaction but the other three species did. All three showed greatest correlation to these variables at different times.

3.4 Discussion

Understanding the ways in which annual variability and environmental variables can shape mosquito abundance and community interactions is critical to understanding the population dynamics of nuisance and vector species, whether to predict population increases or to streamline management strategies to reduce health risks. Our study used systematic weekly sampling of mosquitoes in 2014 and 2015 to assess community structure and dominance and phenological patterns of abundance. Using ordination methods, community structure was compared between years and across three habitat types (suburban, field, forest) and we analysed the community structure from the start to the end of each year by examining the relative proportion of the most dominant species in our communities. We also assessed effects of temperature and precipitation on mosquito populations and communities

3.4.1 Community structure

Despite variation in mosquito communities from year to year, the habitat types remained distinct and significantly different from each other, except for suburban sites (Fig. 3.2; Table 2.1). Variability in mosquito assemblage structure between years was also observed by Schäfer et al. (2008), who noted a high degree of variability between years, but as we see with suburban sites, some habitats show similarity from one year to the next. Suburban habitat is unique in that it contains many peridomestic and man-made water sources (gutters, containers, etc.) that are favorable breeding sites for a limited number of species (Hribar et al., 2001; Townroe & Callaghan, 2014) and these species do not travel very far after emerging (Bellini et al., 2010; Hamer et al., 2014). Field and forest habitat had a much wider range of species and greater abundance and subsequently more inter annual variability when compared to suburban habitat.

3.4.2 Phenology

Peak abundance in overall mosquito numbers was observed in early July in 2014 and in mid-July and mid-August in 2015, with the greatest peak in August (Fig.3.4). Early peaks in both years occurred at approximately similar times. Variation in peak abundance can occur from year to year, sometimes with a single peak or with multiple peaks (Godsey et al., 2010). Lysyk (2010) discovered that *Aedes* spp. showed inter annual differences in the timing of peak abundance, and that seasonal trends were hard to pinpoint. The variability in seasonality and abundance from one year to another can sometimes be explained by stochastic weather such as a single large rainfall event (Godsey et al., 2010) or by the temperature pattern within a given year (Deichmeister & Telang, 2011).

3.4.3 Species level dominance and phenology

Variability in dominance (Fig. 3.3) and phenological patterns (Fig. 3.5) observed at the species level are likely explained by natural history traits and biological requirements unique to each of the species considered. Crans (2004) provides an excellent overview of the overwintering strategies and breeding habitat requirements for all of our focal species. In fact each species defines a different “type” by his classification and are thus

very different strategists. These differing strategies will influence when they can be found and their potential as dominant species. Optimal conditions required for development occur at different times of year and may result in a staggered emergence and possibly explain the differences observed in species dominance partitioning and abundance peaks. For instance, in our two *Aedes* species, *Ae. canadensis* egg hatching is triggered by snowmelt in early spring within shaded forest pools (Carepenter & Lacasse, 1955; Crans 2004). *Ae. vexans*, on the other hand, lay eggs in open-area depressions created in the previous year which hatch following spring rains at a minimum temperature of 10°C (Becker et al., 2003; Crans, 2004; Lysyk, 2010). The number of generations produced by *Ae. vexans* in a year is determined by the number of flood events, of which flooding by rainfall is highly variable and local (Horsfall et al., 1973). *Coquilleltidia perturbans* overwinters as larvae affixed to stems of aquatic vegetation within permanent water bodies (Bosak & Crans, 2002; Crans, 2004) and *Cx. pipiens* overwinters in the adult stage (Crans, 2004; Rinehart et al., 2006). Similar to our findings, Godsey et al. (2010) discovered that most species showed variation in seasonal abundance by year and by site and that the timing of peak abundance as well as the number of peaks observed also varied on a yearly basis.

3.4.4 Environmental variables and lag effects

When looking at all species combined for 2014 and 2015 (Table 3.2), we see that mosquito abundance was significantly influenced by mean weekly temperature values much closer to the date of collection, either during that week (lag 0) in 2014 or one week previous (lag 1) in 2015. Our data support a positive correlation between mosquito activity and temperature. Shand et al. (2016) observed that as time lag increased, the correlation with temperature was lessened, suggesting high correlations of abundance with short term temperature effects. Many studies have identified temperature as a main driver of mosquito abundance and activity and noted significant positive relationships between these factors (DeGroot et al., 2007; Pecoraro et al., 2007; Lysyk, 2010; Deichmeister & Telang, 2011; Ganser & Wisely, 2013; Jacups et al., 2015). DeGroot et al. (2007) noted that mosquito abundance showed significant positive relationships to temperature in all lag intervals from as early as a few days to five weeks, whereas

others show negative relationships further away from the date of collection (Chuang et al., 2011). This shows that the effect of temperature can be variable.

Precipitation is often regarded as limiting the availability of breeding sites, which affects larval success and adult mosquito abundance (Shaman & Day, 2007; Gong et al., 2011). Our results show precipitation typically has a greater effect after longer time intervals. These were at three weeks lag and two weeks lag in 2014 and 2015, respectively (Table 3.2). Similar findings were reported by Chuang et al. (2011) who found that precipitation generally had a greater influence on abundance at lags of 2-3 weeks prior to collection. Our results for the combined effect of temperature and precipitation are not consistent between 2014 and 2015 and the synergistic effects occurred at similar time lags to those of temperature in 2014 and of precipitation in 2015. In 2014, the combined influence of these variables was non-significant as a factor.

3.4.5 Environmental variables and lag effects-species level

At the species level, much variability was observed with respect to how temperature and precipitation affected local abundance (Table 3.3). No clear patterns were observed with *Ae. canadensis*. All relationships observed were significant with the exception of precipitation in 2015. In 2014, a response to all three environmental parameters occurred at a lag of 3 weeks or later, while in 2015, all significant interactions occurred at a lag of zero weeks. *Ae. vexans* demonstrated a positive and significant response to all environmental variables considered. In both years, the greatest response was to the combined effect of temperature and precipitation. In 2014, this mirrored the time lag response for temperature and in 2015, to that of precipitation. This species demonstrates relatively short term response to temperature, suggesting that overall flight activity is tied to temperature. In both years, this species showed more of a long term response to precipitation, a biologically plausible time frame to suggest possible reproductive ties to precipitation events. *Cq. perturbans* showed the fewest correlations with temperature and precipitation. Buckner et al. (2011) found similar results in that weather variables did not reliably predict presence/absence of *Cq. perturbans*. The only

significant relationship existed with temperature at lag 0 in 2014 and all other interactions were weak and non-significant. This was to be expected with precipitation, as this species does not rely on rainfall for development. In 2014, *Cx. pipiens* showed no significant response to any of the environmental variables tested at any of the time lag intervals. The only significant response seen was with temperature and the combined effect of the variables in 2015. We expected more of a response with precipitation, as this species is known to use artificial water holding containers (Becker et al., 2003; Yee, 2008; Vezzani & Albicocco, 2009), but no response was shown in either year. A lack of correlation with precipitation may be explained by artificial breeding pools possibly replenished by human behaviour and not solely by rainfall events (Vezzani, 2007, Naish et al., 2014), or that rainfall may flush larvae from breeding containers (Koenraadt & Harrington, 2008; Deichmeister & Telang, 2011). DeGaetano (2005) demonstrated that trap captures of *Culex* were higher in response to rainfall events occurring beyond the four week time lag used in this study. Temperature is considered a more reliable predictor of *Culex* abundance compared to precipitation (Deichmeister & Telang, 2011), yet only in 2015 was a significant relationship observed, occurring three weeks before trap collection.

3.4.6 Conclusions

Overall, our findings demonstrate that there is a high degree of variability in mosquito communities, phenology, and abundance annually and in response to environmental variables. NMDS ordination shows that between similar habitats, community composition varies annually but that suburban habitat showed less variability versus more natural habitat. Phenological patterns of total mosquito abundance show that peaks typically emerged within the early weeks of July but that the timing of peaks and the number of peaks encountered in a given year was variable and likely tied to the influence of prevailing environmental conditions. Dominance and phenological patterns exhibited by the most abundant species appear to have had less annual variability. Early season species, such as *Ae. canadensis* and *Cq. Perturbans*, were among the first to reach high numbers in both years. Shortly after, the well-known nuisance species *Ae. vexans* was the most dominant species, occupying that position for much of the

summer months. However, timing of peak abundance fluctuated between years. *Culex pipiens* only appeared as a late season species and remained active throughout the latter half of the summer and into autumn, an important consideration due to the medical importance of this species in the transmission of WNV. Analysis of the relationship between abundance and the response to environmental variables reveals a degree of annual variation, but does produce generalized trends. Adult mosquito abundance is tied to temperature over short time intervals in a positive and significant way, suggesting that warmer temperatures can lead to greater mosquito abundance and activity. Precipitation provides a generalized pattern which relates to abundance several weeks before trap collection, suggesting a possible link to reproduction. The clarity of these patterns is not maintained when analysing these responses with the four focal species examined. Although some followed these generalized trends, the different life history traits expressed by these species leads to some clear patterns of association with some variables and not with others, and between year variations were encountered.

Although our data show variability, they reveal biologically plausible patterns which can be used as general guidelines for understanding of how communities change, how these communities are shaped and when and how population fluctuations can occur. Our data reveal patterns for several species of interest, including well known nuisance species and potential disease vectors. This information leads to some basic assumptions, but for more concrete conclusions to be drawn, long term data, both with respect to mosquito communities and meteorology should be used to generate more long term and thus, clearer patterns.

3.5 References

- Becker, N., Petrić, D., Zgomba, M., Boase, C., Dahl, C. Lane, J., & Kaiser, A. (2003). Mosquitoes and their control. Springer. New York, NY. 577 pp.
- Becker, N. (2008). Influence of climate change on mosquito development and mosquito-borne diseases in Europe. *Parasitology Research*, 103(1), 19-28.

- Bellini, R., Albieri, A., Balestrino, F., Carrieri, M., Porretta, D., Urbanelli, S., Calvitti, M., Moretti, R., & Maini, S. (2010). Dispersal and survival of *Aedes albopictus* (Diptera: Culicidae) males in Italian urban areas and significance for sterile insect technique application. *Journal of Medical Entomology*, 47(6), 1082-1091.
- Bhatt, S., Gething, P. W., Brady, O. J., Messina, J. P., Farlow, A. W., Moyes, C. L., Drake, J. M., Brownstein, J. S., Hoes, A. G., Sankoh, O., Myers, M. F., George, D. B., Jaenisch, T., Wint, W. G. R., Simmons, C. P., Scott, T. W., Farrar, J. J., & Hay, S. I. (2013). The global distribution and burden of dengue. *Nature*, 496(7446), 504-507.
- Bicout, D. J., & Sabatier, P. (2004). Mapping Rift Valley fever vectors and prevalence using rainfall variations. *Vector-borne and Zoonotic Diseases*, 4(1), 33-42.
- Bosak, P. J., & Crans, W. J. (2002). The structure and function of the larval siphon and spiracular apparatus of *Coquillettidia perturbans*. *Journal of the American Mosquito Control Association-Mosquito News*, 18(4), 280-283.
- Buckner, E. A., Blackmore, M. S., Golladay, S. W., & Covich, A. P. (2011). Weather and landscape factors associated with adult mosquito abundance in southwestern Georgia, USA. *Journal of Vector Ecology*, 36(2), 269-278.
- Calisher, C. H. (1994). Medically important arboviruses of the United States and Canada. *Clinical microbiology reviews*, 7(1), 89-116.
- Canadian Climate Impacts and Adaptation Research Network-Ontario (2002). Accessed November 2016. Retrieved from: <http://www.parl.gc.ca/content/sen/committee/372/agri/power/ontario-e.htm>
- Carpenter, S. J., & LaCasse, W. J. (1955). *Mosquitoes of North America*. University of California Press. Berkeley, California. 360 pp.
- (CDC) Centres for disease control and prevention. (2016). Accessed November 2016. Retrieved from: <https://www.cdc.gov/lac/gen/qa.html>
- Chuang, T. W., Hildreth, M. B., Vanroekel, D. L., & Wimberly, M. C. (2011). Weather and land cover influences on mosquito populations in Sioux Falls, South Dakota. *Journal of Medical Entomology*, 48(3), 669-679.

- Ciota, A. T., Matacchiero, A. C., Kilpatrick, A. M., & Kramer, L. D. (2014). The effect of temperature on life history traits of *Culex* mosquitoes. *Journal of Medical Entomology*, 51(1), 55-62.
- Clements A. N. (1992). The Biology of Mosquitoes: Growth, nutrition and reproduction. Chapman & Hall. London. 536 pp.
- Crans, W. J. (2004). A classification system for mosquito life cycles: life cycle types for mosquitoes of the northeastern United States. *Journal of Vector Ecology*, 29, 1-10.
- Darsie Jr, R. F., & Ward, R. A. (2005). Identification and geographical distribution of the mosquitoes of North America, north of Mexico. *Journal of the American Mosquito Control Association*, 21(1). University Press of Florida, Gainesville, FL. 383 pp.
- DeGaetano, A. T. (2005). Meteorological effects on adult mosquito (*Culex*) populations in metropolitan New Jersey. *International Journal of Biometeorology*, 49(5), 345-353.
- DeGroote, J., Mercer, D. R., Fisher, J., & Sugumaran, R. (2007). Spatiotemporal investigation of adult mosquito (Diptera: Culicidae) populations in an eastern Iowa county, USA. *Journal of Medical Entomology*, 44(6), 1139-1150.
- Deichmeister, J. M., & Telang, A. (2011). Abundance of West Nile virus mosquito vectors in relation to climate and landscape variables. *Journal of Vector Ecology*, 36(1), 75-85.
- Environment Canada (2016). Government of Canada. Historical Climate Data. Accessed April 2016. Retrieved from http://climate.weather.gc.ca/historical_data/search_historic_data_e.html
- EPA - Environmental Protection Agency: Mosquito Life Cycle (2016). Accessed October 2016. Retrieved from: <https://www.epa.gov/mosquitocontrol/mosquito-life-cycle>
- Ewing, D. A., Cobbold, C. A., Purse, B. V., Nunn, M. A., & White, S. M. (2016). Modelling the effect of temperature on the seasonal population dynamics of temperate mosquitoes. *Journal of Theoretical Biology*, 400, 65-79.

- Fontenille, D., Lochouart, L., Diagne, N., Sokhna, C., Lemasson, J. J., Diatta, M., Konate, L., Faye, F., Rogier, C., & Trape, J. F. (1997). High annual and seasonal variations in malaria transmission by anophelines and vector species composition in Dielmo, a holoendemic area in Senegal. *American Journal of Tropical Medicine and Hygiene*, 56(3), 247-253.
- Ganser, C., & Wisely, S. M. (2013). Patterns of spatio-temporal distribution, abundance, and diversity in a mosquito community from the eastern Smoky Hills of Kansas. *Journal of Vector Ecology*, 38(2), 229-236.
- Godsey Jr, M. S., Burkhalter, K., Delorey, M., & Savage, H. M. (2010). Seasonality and time of host-seeking activity of *Culex tarsalis* and floodwater *Aedes* in northern Colorado, 2006–2007. *Journal of the American Mosquito Control Association*, 26(2), 148-159.
- Gong, H., DeGaetano, A. T., & Harrington, L. C. (2011). Climate-based models for West Nile *Culex* mosquito vectors in the Northeastern US. *International Journal of Biometeorology*, 55(3), 435-446.
- Gould, E. A., & Higgs, S. (2009). Impact of climate change and other factors on emerging arbovirus diseases. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 103(2), 109-121.
- Gubler, D. J. (2010). The global threat of emergent/re-emergent vector-borne diseases. In *Vector Biology, Ecology and Control* (pp. 39-62). Springer. Netherlands.
- Haddow, A. D. (2009). The incidence risk, clustering, and clinical presentation of La Crosse virus infections in the eastern United States, 2003–2007. *PLoS One*, 4(7), e6145.
- Hamer, G. L., Anderson, T. K., Donovan, D. J., Brawn, J. D., Krebs, B. L., Gardner, A. M., Ruiz, M. O., Brown, W. M., Kitron, U. D., Newman, C. M., Goldberg, T. L., & Walker, E. D. (2014). Dispersal of adult *Culex* mosquitoes in an urban West Nile virus hotspot: a mark-capture study incorporating stable isotope enrichment of natural larval habitats. *PLoS Neglected Tropical Diseases*, 8(3), e2768.
- Hayes, E. B., & Gubler, D. J. (2006). West Nile virus: Epidemiology and clinical features of an emerging epidemic in the United States*. *Annual Review of Medicine*, 57, 181-194.

- Horsfall, W. R., Fowler Jr, H. W., Moretti, L. J., & Larson, J. R. (1973). Bionomics and embryology of the inland floodwater mosquito *Aedes vexans*. University of Illinois Press, Urbana, Ill. 211 pp.
- Hribar, L. J., Smith, J. M., Vlach, J. J., & Verna, T. N. (2001). Survey of container-breeding mosquitoes from the Florida Keys, Monroe County, Florida. *Journal of the American Mosquito Control Association*, 17(4), 245-248.
- Hu, W., Tong, S., Mengersen, K., & Oldenburg, B. (2006). Rainfall, mosquito density and the transmission of Ross River virus: A time-series forecasting model. *Ecological Modelling*, 196(3), 505-514.
- loos, S., Mallet, H. P., Goffart, I. L., Gauthier, V., Cardoso, T., & Herida, M. (2014). Current Zika virus epidemiology and recent epidemics. *Medecine et Maladies Infectieuses*, 44(7), 302-307.
- Jacups, S. P., Carter, J., Kurucz, N., McDonnell, J., & Whelan, P. I. (2015). Determining meteorological drivers of salt marsh mosquito peaks in tropical northern Australia. *Journal of Vector Ecology*, 40(2), 277-281.
- Koenraadt, C. J. M., & Harrington, L. C. (2008). Flushing effect of rain on container-inhabiting mosquitoes *Aedes aegypti* and *Culex pipiens* (Diptera: Culicidae). *Journal of Medical Entomology*, 45(1), 28-35.
- Lysyk, T. J. (2010). Species abundance and seasonal activity of mosquitoes on cattle facilities in southern Alberta, Canada. *Journal of Medical Entomology*, 47(1), 32-42.
- McMichael, A. J., Woodruff, R. E., & Hales, S. (2006). Climate change and human health: present and future risks. *Lancet*, 367(9513), 859-869.
- Naish, S., Dale, P., Mackenzie, J. S., McBride, J., Mengersen, K., & Tong, S. (2014). Climate change and dengue: a critical and systematic review of quantitative modelling approaches. *BMC Infectious Diseases*, 14(1), 1.
- Oksanen, J. 2015. Vegan: an introduction to ordination. University of Oulu. Retrieved from: <http://cran.r-project.org/web/packages/vegan/vignettes/intro-vegan.pdf>
- Paaijmans, K. P., Imbahale, S. S., Thomas, M. B., & Takken, W. (2010). Relevant microclimate for determining the development rate of malaria mosquitoes and possible implications of climate change. *Malaria Journal*, 9(1), 1.

- Pecoraro, H. L., Day, H. L., Reineke, R., Stevens, N., Withey, J. C., Marzluff, J. M., & Meschke, J. S. (2007). Climatic and landscape correlates for potential West Nile virus mosquito vectors in the Seattle region. *Journal of Vector Ecology*, 32(1), 22-28.
- Petersen, E., Wilson, M. E., Touch, S., McCloskey, B., Mwaba, P., Bates, M., Dar, O., Mattes, F., Kidd, M., Ippolito, G., Azhar, E. I., & Zumla, A. (2016). Rapid spread of Zika virus in the Americas-Implications for public health preparedness for mass gatherings at the 2016 Brazil Olympic Games. *International Journal of Infectious Diseases*, 44, 11-15.
- Ponçon, N., Toty, C., L'ambert, G., Le Goff, G., Brengues, C., Schaffner, F., & Fontenille, D. (2007). Population dynamics of pest mosquitoes and potential malaria and West Nile virus vectors in relation to climatic factors and human activities in the Camargue, France. *Medical and Veterinary Entomology*, 21(4), 350-357.
- Rinehart, J. P., Robich, R. M., & Denlinger, D. L. (2006). Enhanced cold and desiccation tolerance in diapausing adults of *Culex pipiens*, and a role for Hsp70 in response to cold shock but not as a component of the diapause program. *Journal of Medical Entomology*, 43(4), 713-722.
- Schäfer, M. L., Lundström, J. O., & Petersson, E. (2008). Comparison of mosquito (Diptera: Culicidae) populations by wetland type and year in the lower River Dalälven region, Central Sweden. *Journal of Vector Ecology*, 33(1), 150-157.
- Shaman, J., & Day, J. F. (2007). Reproductive phase locking of mosquito populations in response to rainfall frequency. *PLoS ONE*, 2(3), e331.
- Shand, L., Brown, W. M., Chaves, L. F., Goldberg, T. L., Hamer, G. L., Haramis, L., Kitron, E. D. & Ruiz, M. O. (2016). Predicting West Nile virus infection risk from the synergistic effects of rainfall and temperature. *Journal of Medical Entomology*, 53(4), 935-944.
- The Canadian Biodiversity website. Redpath Museum, McGill University. Accessed September 2016. Retrieved from:
<http://canadianbiodiversity.mcgill.ca/english/ecozones/mixedwoodplains/mixedwoodplains.htm>

- Thielman, A. C., & Hunter, F. F. (2007). *A photographic key to adult female mosquito species of Canada (Diptera: Culicidae)*. Canadian Journal of Arthropod Identification, 4, 1-117.
- Tolle, M. A. (2009). Mosquito-borne diseases. *Current Problems in Pediatric and Adolescent Health Care*, 39(4), 97-140.
- Townroe, S., & Callaghan, A. (2014). British container breeding mosquitoes: the impact of urbanisation and climate change on community composition and phenology. *PloS ONE*, 9(4), e95325.
- Vezzani, D. (2007). Review: Artificial container-breeding mosquitoes and cemeteries: a perfect match. *Tropical Medicine & International Health*, 12(2), 299-313.
- Vezzani, D., & Albicocco, A. P. (2009). The effect of shade on the container index and pupal productivity of the mosquitoes *Aedes aegypti* and *Culex pipiens* breeding in artificial containers. *Medical and Veterinary Entomology*, 23(1), 78-84.
- Weaver, S. C. (2014). Arrival of chikungunya virus in the new world: prospects for spread and impact on public health. *PLoS Neglected Tropical Diseases*, 8(6), e2921.
- Week Number. Retrieved from: www.week-number.net
- Wilkerson, R. C., Linton, Y. M., Fonseca, D. M., Schultz, T. R., Price, D. C., & Strickman, D. A. (2015). Making mosquito taxonomy useful: a stable classification of tribe Aedini that balances utility with current knowledge of evolutionary relationships. *PLoS ONE*, 10(7), e0133602.
- Williams, R. E. (2009). *Veterinary entomology: livestock and companion animals*. CRC Press, Taylor & Francis Group. Boca Raton. 376 pp.
- Wood, D. M., Dang, P. T., & Ellis, R. A. (1979). The insects and arachnids of Canada. Part 6. The mosquitoes of Canada. Diptera: Culicidae. Canadian Government Publishing Centre. Hull, Quebec. 390 pp.
- World Health Organization (WHO) 2016: Accessed October 2016. Retrieved from: <http://www.who.int/mediacentre/factsheets/fs387/en/>
- Yee, D. A. (2008). Tires as habitats for mosquitoes: a review of studies within the eastern United States. *Journal of Medical Entomology*, 45(4), 581-593.

3.6 Tables and Figures

Table 3.1. PERMANOVA results for the interactions of year and habitat for 2014 & 2015. P-values in bold are adjusted P-values following Post Hoc analysis.

Interaction	F	R ²	P
Year	34.03	0.2357	<0.001*
Habitat	35.75	0.4952	<0.001*
Year*Habitat	2.42	0.0335	0.023*
Suburb vs. Forest	22.69	0.4306	0.003*
Suburb vs. Field	12.19	0.4038	0.003*
Forest vs. Field	18.26	0.4126	0.003*
2014 Suburb vs. 2015 Suburb	10.05	0.5012	0.060
2014 Forest vs. 2015 Forest	33.77	0.6523	0.015*
2014 Field vs. 2015 Field	3.55	0.372	0.015*

*= significant P-values

Table 3.2. Linear model fit for mosquito abundance against mean weekly temperature, total weekly precipitation, and MW temperature + TW precipitation for 2014 & 2015. Highest R² values appear in shaded boxes. Significant values indicated by (*).

Week lag	Mean Weekly Temperature					Total Precipitation					MW. Temperature + Tot. Precipitation				
	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
Adjusted R ²															
2014	0.3549*	0.0794	-0.0268	-0.0764	0.0543	-0.0755	0.0230	0.0247	0.257*	-0.0010	0.2687	0.1187	-0.0606	0.2625	0.1911
2015	0.185*	0.2837*	0.1299*	0.0642	0.0395	-0.0435	-0.0338	0.1931*	0.0671	-0.0288	0.1556	0.2523*	0.2927*	0.1099	0.0042

Table 3.3. Results from linear model fitting exploring the effect of environmental variables on abundance of four focal species using mean weekly temperature, total weekly precipitation and their combined effect across a 4-week lag period. Values in boldface represent the highest R² values for each species and (*) indicates a significant P-value (P<0.05).

2014	week lag	Mean Weekly Temperature					Total Weekly Precipitation					MWTemp + TW Precip.				
		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Ae. canadensis</i>		0.2294*	0.01272	-0.048	-0.06999	0.2307*	-0.06941	0.09412	0.02566	0.3969*	-0.02005	0.1673	0.0901	-0.0289	0.3617*	0.1994
<i>Cq. perturbans</i>		0.2541*	0.08901	0.05628	-0.001126	-0.01173	-0.04828	-0.03375	-0.07596	0.05038	0.1647	0.2419	0.04276	-0.02	0.1389	0.1379
<i>Ae. vexans</i>		0.2659*	0.04433	-0.06111	-0.05476	-0.03498	-0.02848	0.07599	-0.07051	0.06328	0.2523*	0.2817*	0.1021	-0.1435	0.0623	0.2107
<i>Cx. pipiens</i>		0.06834	-0.03452	0.1297	0.07817	0.09693	0.06919	0.03399	0.01017	-0.02846	-0.07592	0.1757	-0.0146	0.1644	0.015	0.0288
2015		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Ae. canadensis</i>		0.2535*	0.1014	0.0533	0.03002	0.01194	-0.03529	-0.00278	-0.00736	0.02046	0.1047	0.2196*	0.087	0.0351	0.0356	0.1026
<i>Cq. perturbans</i>		0.08814	0.03683	0.01401	-0.01963	-0.03453	0.0152	-0.02322	-0.02695	0.04174	0.01681	0.0816	0.0058	-0.0202	0.0122	-0.0232
<i>Ae. vexans</i>		0.1345*	0.2725*	0.1469*	0.1039	0.09969	-0.009102	-0.04022	0.303*	0.00396	-0.03742	0.1667*	0.2395*	0.4135*	0.0924	0.0599
<i>Cx. pipiens</i>		0.1564*	0.2402*	0.2074*	0.2719*	0.1755*	-0.02405	0.0428	0.03243	0.05076	-0.001111	0.1223	0.263*	0.2208*	0.2954*	0.1624*

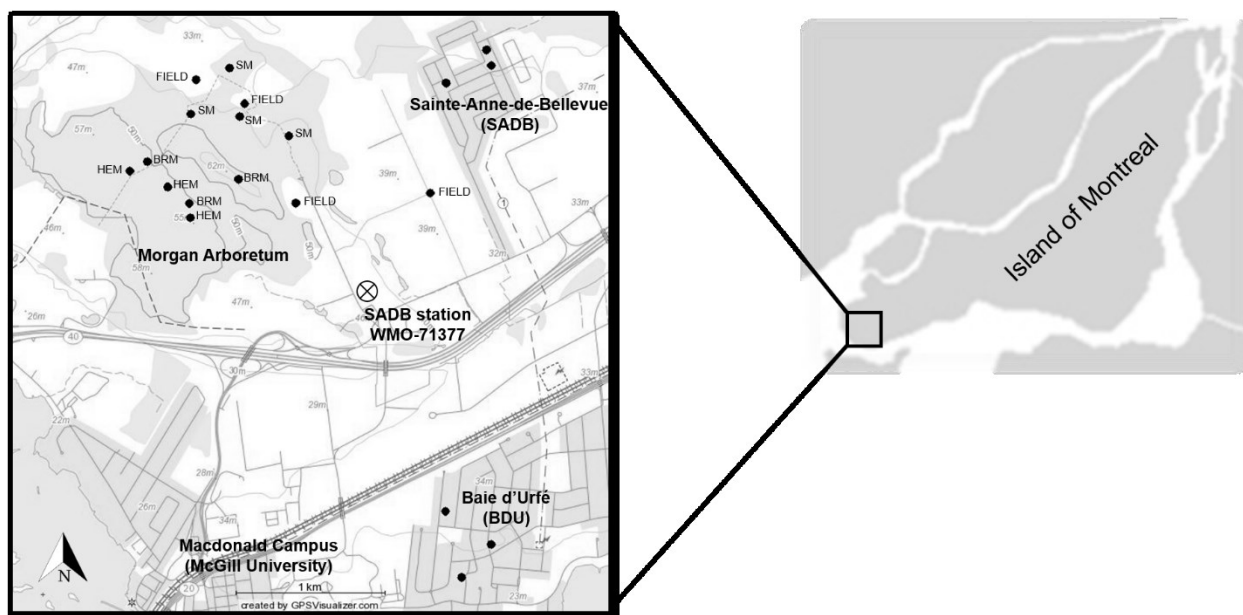


Figure 3.1. Map of the study area showing trap locations and location of the Sainte-Anne-de-Bellevue Meteorological station located on the Western tip of the island of Montreal, Quebec, Canada. Suburban sites: Baie d'Urfé (BDU) and Sainte-Anne-de-Bellevue (SADB); Forest sites: Sugar Maple (SM), Beech-Red Maple (BRM) and Eastern Hemlock (HEM); Field sites (FIELD).

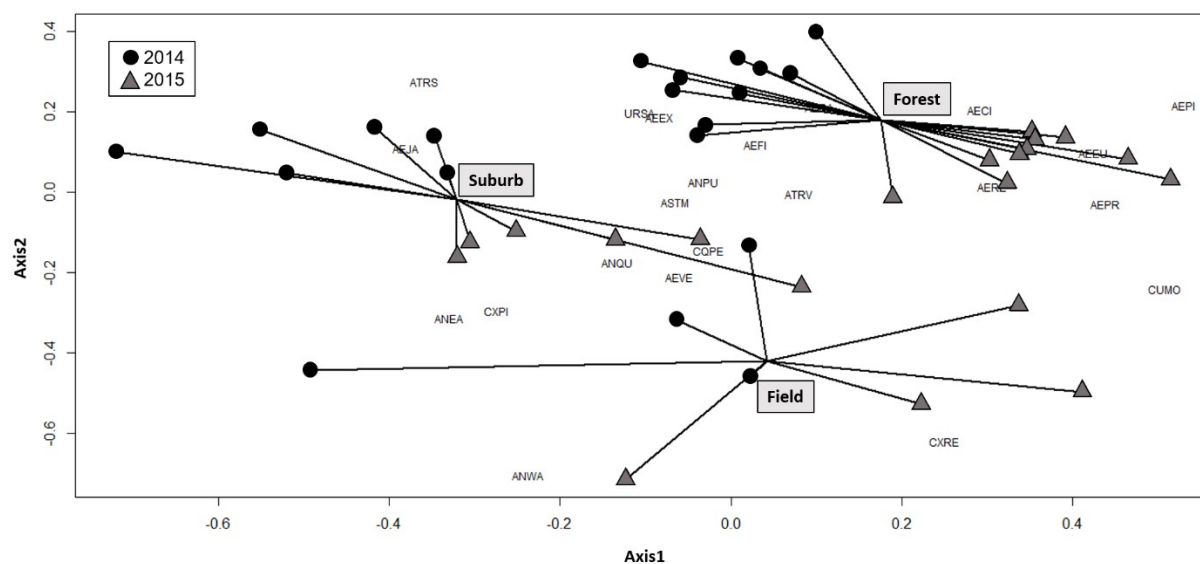


Figure 3.2. NMDS ordination showing comparison on mosquito community structure across both sampling seasons (Stress: 0.0987). Four letter acronyms represent individual species (ex. AVEE = *Aedes vexans*).

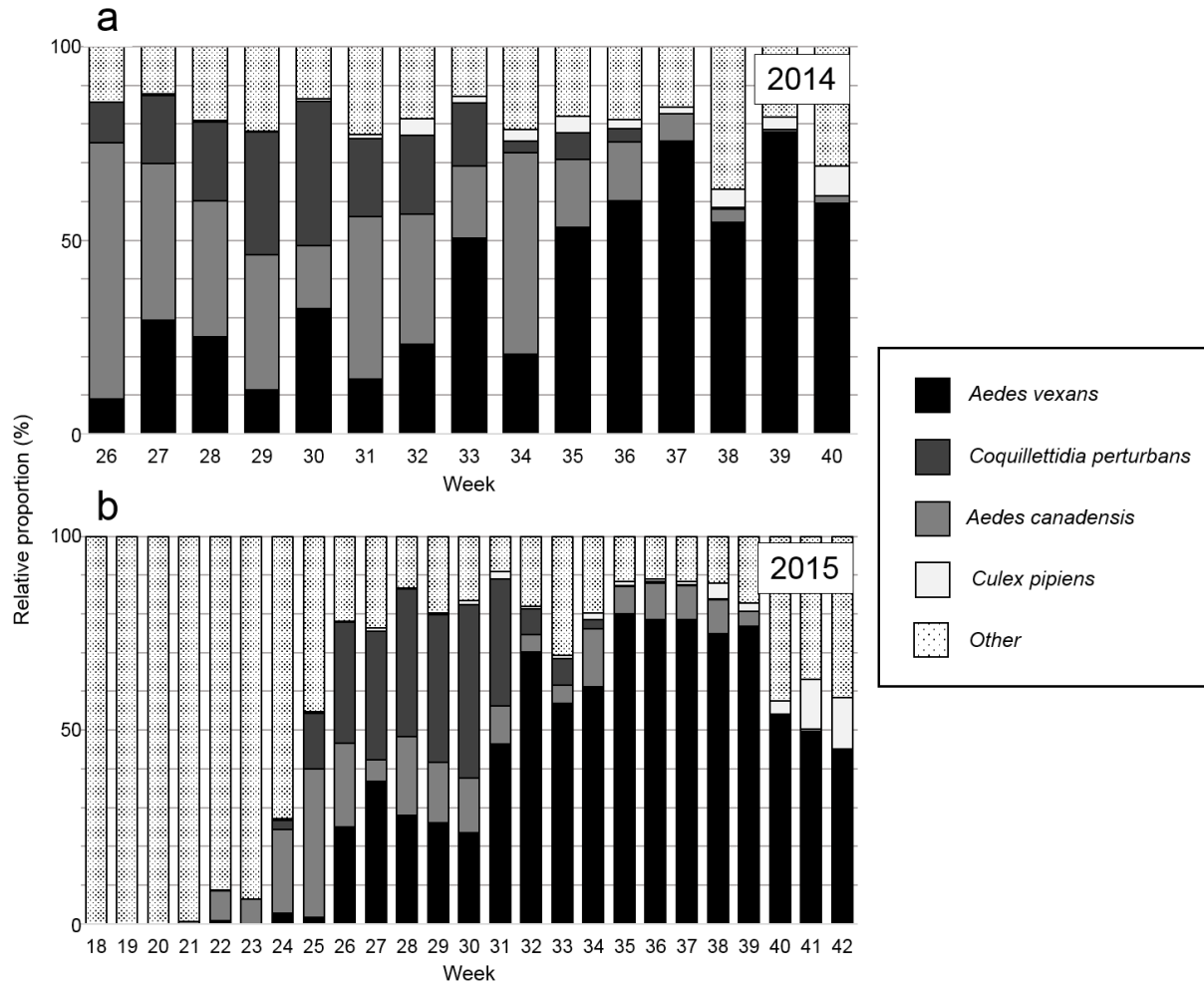


Figure 3.3. Seasonal community structure as shown by relative dominance of the four focal species compared to all other species collected in both 2014 (a) and 2015 (b).

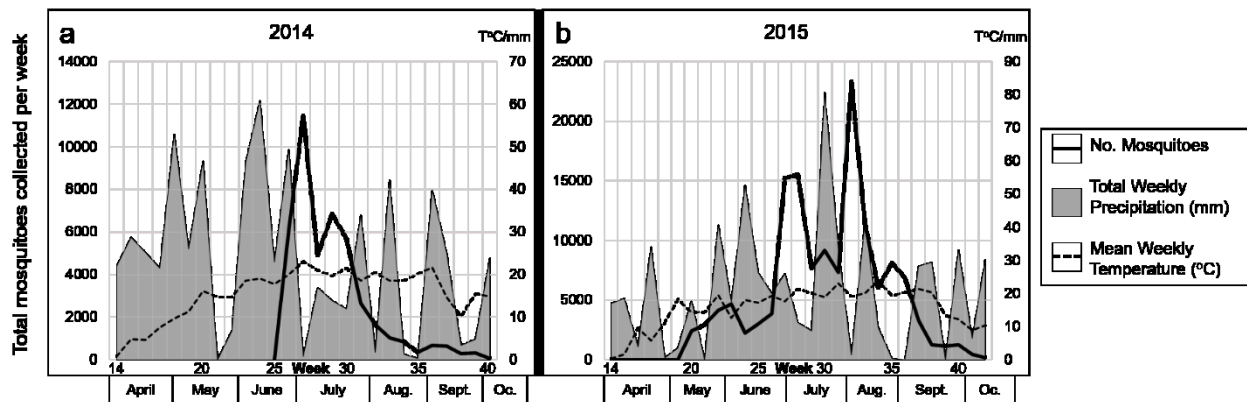


Figure 3.4. Weekly mosquito abundance, total weekly precipitation, and mean weekly temperature for 2014 (a) and 2015 (b).

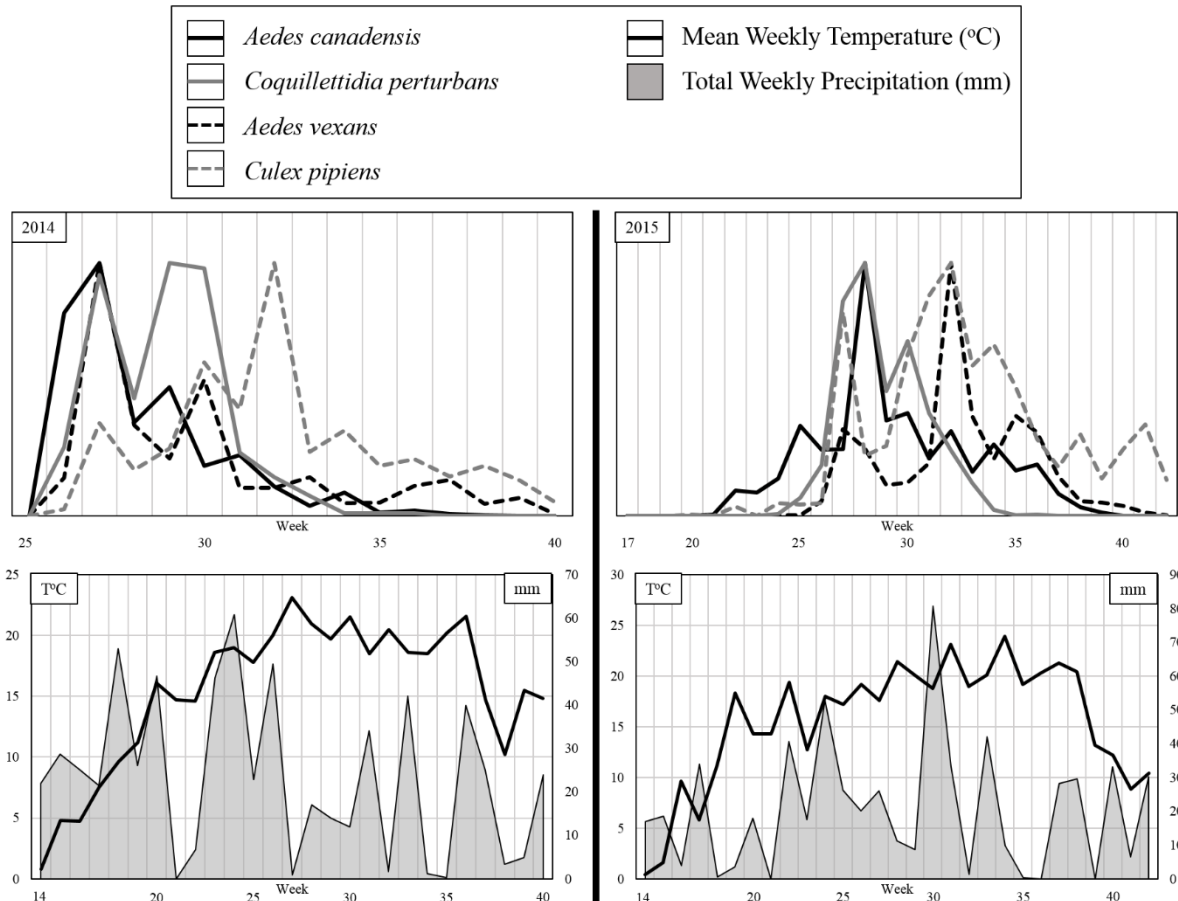


Figure 3.5. Patterns of species abundance based on proportion of maximum abundance for our four focal species in 2014 (left) and 2015 (right). Environmental parameters, temperature and precipitation beginning in week 14 and terminating with the end of the sampling season can be seen below.

3.7 Connecting Statement

Chapter 3 provided details about annual variability with respect to community structure and relative abundance of dominant species, as well as providing information on how the variables of temperature and precipitation act to shape mosquito populations over weekly time lags. It provides valuable information about the timing of peak emergence and specific links between climate and the populations and phenology of important vector and nuisance species in the West Island of Montreal. It also reveals just how variable mosquito ecology can be. The final Chapter of this thesis is a general summary of findings and conclusions.

Thesis Summary and Conclusion

This thesis established some important baseline data for mosquito ecology in the western portion of the island of Montreal, which until now, has not had an extensive ecological investigation of adult mosquitoes. Moving forward, the information gathered here can be of use to the installation and streamlining of surveillance and monitoring programmes as well as improving efforts in mosquito control with respect to West Nile Virus, a relatively recent emerging infectious disease in southern Quebec. The information provided about habitats and environmental variables may be of use in future modeling of mosquito populations in the context of global climate change and subsequently the colonization by invasive species, range expansion of more southern species and the implications this may have on nuisance and vector potential.

Chapter 1 introduced the history of mosquito ecology in North America while introducing some of the considerations with respect to sampling, modeling and novel techniques in identification and cataloguing species. Chapter 2 explored the effect of habitat on shaping mosquito communities and provides some clear patterns with respect to this relationship. It showed that different habitats produced distinct mosquito community structure, an important finding in a region where a multitude of different habitats types lie in close proximity to one another. Another important finding is that when we compare habitats with similar overall structure, for instance two different suburban municipalities, the community structure is similar, suggesting that small scale, or microhabitat elements are playing an important role in how mosquito communities are structured in these habitats. We saw that more natural habitats like fields and forests can support greater abundance and diversity than more disturbed habitats such as suburban backyards. However, it appears that suburban habitats are the preferred habitat for *Culex pipiens*, and important vector species in the spread of West Nile virus. This finding will likely be of importance for mosquito management.

Chapter 3 explored the temporal variation in mosquito community structure by examining the differences in communities collected from similar habitats but across a two year period. This shows that habitat still generates distinct communities regardless of the year of investigation but that from one year to the next, these communities also

show variability. Patterns of species dominance focusing on the most abundant species shows that throughout the year, turnover is occurring with respect to which species are the most abundant at a particular time. These patterns were maintained in both years suggesting that species natural history and resource requirements likely drives seasonality and relative abundance. The phenology of dominant species reveals that species tend to reach peak abundance at similar periods in each year, allowing for basic classifications as “early season” or “late season” species. Interesting observations are that *Ae. vexans*, an important nuisance species emerges relatively early and is a consistently dominant species in both years. The medically important species, *Culex pipiens* shows trends toward late season emergence and remains active later into the season. Phenological patterns of total mosquito abundance reveal that although peak abundance tends to occur at similar times of year (early July) the exact timing of peaks and the number of peaks can vary annually, likely explained by environmental conditions. The examination of the interaction between environmental variables and mosquito abundance produced some interesting trends. While utilizing a lag effect model, we produced some results that seem biologically plausible with respect to mosquito abundance and reliance on environmental conditions. We observe that in general, mosquito abundance whether at the species level or when considering all species combined, typically respond to temperatures over short time lags. This suggests that warmer temperatures tend to increase mosquito flight activity and likely biting activity, an important consideration when considered in the context of biting rate or disease transmission. When paired with precipitation, our models reveal a longer time lag relationship, generally in the area of 2-3 weeks. This result may shine some light on the relationship between mosquito reproductive fitness in response to precipitation events on a local scale. Although these generalized patterns were observed, some variability still exists with certain species between years.

Although our results provide some insight into the drivers of mosquito community structure and populations dynamics, there remain many unanswered questions. Research such as this provides a wealth of data at a local scale, but extrapolating this data to other regions is difficult and thus there exists, and will remain for a long time, a need to study mosquito ecology.