EFFECTS OF HABITAT SIZE AND LAND USE ON DIVERSITY OF HIGHER DIPTERA IN EASTERN NEARCTIC PEATLANDS

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PREFACE

This thesis contains three chapters.

Chapter 1

This chapter is a general introduction, literature review and outline of research objectives and hypotheses.

Chapter 2

This chapter is a manuscript in preparation for submission to a refereed journal:

Moores, A.M.A., J. Savage and T.A. Wheeler. Effects of habitat size and land use on diversity of higher Diptera in temperate eastern Nearctic peatlands.

Chapter 3

This chapter is a general conclusion for the thesis.

CONTRIBUTION OF AUTHORS

All authors contributed to the design of the study presented in Chapter 2. Field sampling, preparation and identification of specimens, data analysis and the written results were performed by A.M.A. Moores. J. Savage and T.A. Wheeler supervised the research, provided equipment, facilities and financial support for field work and also edited all chapters of this thesis.

ABSTRACT

The effects of biotic and abiotic characteristics on Schizophora (Diptera) assemblages in six temperate eastern Nearctic bogs were examined. The main objectives were to investigate the impact of bog size, vegetation structure and surrounding land use on Schizophora diversity and species composition. More than 380 species of Schizophora were collected, indicating that these bogs support a diverse Diptera community. Vegetation structure and land use within a 1500 m radius around the sampling location significantly influenced the species compositions and explained the diversity patterns found at the sites. Bog size did not have a significant impact on species richness, possibly due to the flow of non-bog restricted species from the surrounding landscape. From these results, it was concluded that conservation strategies in eastern Nearctic bogs should promote intermediate levels of agriculture and forested landscape up to 1500 m around a bog in order to support healthy ecosystems with high Schizophora diversity.

RÉSUMÉ

Les effets de plusieurs facteurs biotiques et abiotiques sur les assemblages de Schizophora (Diptera) de six tourbières situées dans la zone tempérée de l'est de la région néarctique ont été examinés. Les objectifs généraux de ce projet étaient d'étudier les impacts de la superficie des tourbières, la structure de la végétation ainsi que l'utilisation des terres avoisinantes sur la composition et la diversité des assemblages de mouches schizophores.

Plus que 380 espèces de Schizophora ont été échantillonnées, indiquant que ces tourbières supportent une communauté de diptères diverse. La structure de végétation a chaque site et l'utilisation des terres environnantes jusqu'à 1500 m des sites d'échantillonnage ont significativement influencé la composition des espèces et expliqué les patrons de diversité inhérent aux sites. La superficie des tourbières n'a pas eu d'impact significatif sur le nombre d'espèces, possiblement en raison du mouvement des espèces du paysage environnant qui ne sont pas restreintes aux tourbières. Ces résultats indiquent que les stratégies de conservation dans les tourbières de l'est de la région néarctique devraient promouvoir le maintient d'un niveau intermédiaire d'intensité agricole ainsi que des terres boisées dans un rayon allant jusqu'à 1500 m autour des tourbières pour maintenir des écosystèmes sains supportant une importante diversité de mouches schizophores.

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

Introduction

Scientists and the general public are becoming increasingly aware of a need for the conservation of biological diversity in natural ecosystems. Habitat loss caused by agriculture and urban development has been identified as the leading threat to terrestrial organisms in North America (Wilcove et al. 1998, Venter et al. 2006). Anthropogenic land use has led to a fragmented and modified landscape, creating an overall decline in biodiversity in some regions (Sinclair et al. 1995, Niemelä et al. 2000) which can in turn lead to a decline in ecosystem functions (Attwood et al. 2008).

Peatlands in the temperate zone of North America have been greatly impacted by anthropogenic disturbance. For many years, these habitats were regarded as ‘wastelands’ and routinely drained for agricultural fields, urban developments, mined for peat and used as landfill sites. It is now known that these ecosystems perform a multitude of ecological functions and provide a habitat for many plants and animals, including insects.

Members of the order Diptera (true flies) are especially diverse and abundant in southern Canadian peatlands (Blades and Marshall 1994, Marshall 1994, Grégoire Taillefer 2008). Flies have short generation times; can be sensitive to habitat changes and large sample sizes can be easily obtained, making them useful indicators of an ecosystem’s health (McGeoch 1998). Additionally, flies are practical to use in conservation and ecological projects as they have large population sizes, have a diverse trophic ecology and are easy to obtain and preserve. Finally, true flies are extremely diverse, with the order containing approximately 10% of all described metazoan species. In spite of such high diversity, they are often ignored in ecological studies, primarily because the high species diversity and a lack of available taxonomic expertise makes species indentification difficult or impossible for non-specialists.

Wetlands in North America

A wetland occurs where the water table is near, level with or exceeds the surface of the land. Wetlands are further characterized as being waterlogged for enough time that the soil becomes adapted to water and hydrophytic vegetation grows (Bélanger et al. 2006). Approximately 14% of Canada's land area and 5.5% of land area in the U.S. is comprised of wetlands (Gillespie et al. 1991, Dahl 2000). The National Wetlands Working Group (1997) defines five classes of wetland based on soil, hydrological and vegetation properties: shallow water wetlands, swamps, marshes, bogs and fens.

Shallow water ecosystems are semi-permanent or permanent wetlands with large areas of standing or flowing water, found in the transitional zone between saturated wetlands (i.e. swamp, marsh, bog or fen) and aquatic ecosystems (i.e. lakes) (Bélanger et al. 2006). Known by such names as oxbows, ponds and pools, they are further characterized as having less than 25% rooted vegetation along the margins and open water vegetation consisting of rooted, submerged or floating hydrophytic plants (Keys 1992). Swamps are distinguished as wetlands with standing or gently flowing water and are often associated with rivers and lakes. They can be permanently or seasonally inundated, though the substrate is consistently wet as the water table or at or near the surface. They occur on peat and mineral soils and generally have over 30% cover of trees, herbs, shrubs and mosses (Keys 1992, Bélanger et al. 2006). Marshes are the most common form of wetland in North America and can be freshwater or coastal (i.e. saline) (Bélanger et al. 2006). Moisture is obtained through inflow, precipitation and groundwater and the water level fluctuates throughout the year due to tides, seepage, evapotranspiration and flooding. Marshes are mineral wetlands and support a variety of vegetation like reeds, rushes, grasses, sedges, shrubs, broad-leaved macrophytes and non-vascular plants like mosses and algae (Bélanger et al. 2006).

Wetland ecosystems where plant production exceeds decomposition resulting in an accumulated peat layer of at least 40 cm in depth are collectively called peatlands (Keys 1992) and are subdivided into two classes: bogs and fens. Bogs are characterized by a layer of peat, usually between 3-5 m thick and a water table that is at or near the surface. Bogs are ombrotrophic*,* meaning the primary source of water is precipitation (in the form of rain, fog or snow) which creates a highly acidic environment with a pH generally between 4 and 4.8 (Gorham and Janssens 1992). The acidity is further augmented from acid ions released during the decomposition of *Sphagnum* mosses and peat (Bélanger et al. 2006). Owing to their acidic nature and sole source of water, bogs are nutrient poor and consequently have low species diversity compared to other habitats (Keys 1992) and dominant vegetation, like ericaceous shrubs and *Sphagnum* mosses, tend to be acidophilic. Fens often superficially resemble bogs, but are minerotrophic, therefore receive moisture from groundwater, surface runoff and precipitation. The water table fluctuates and seeps slowly through the surrounding soil and into the peat, so fens are more nutrient-rich and alkaline than bogs, resulting in higher overall diversity (Bélanger et al. 2006). An array of vegetation, such as reeds, grasses, sedges and *Sphagnum* species are supported in fens (Keys 1992, Rydin and Jeglum 2006).

Importance of peatlands

Peatlands are responsible for many significant ecological processes that not only affect the environment on a regional scale, but also on a global scale (Moore 2002). It has been estimated that 30% of terrestrial carbon is contained within the earth's peatlands (Hilbert et al. 2000) and acting as carbon sinks, these ecosystems are noted for their importance in the global biogeochemical cycle of carbon, carbon dioxide and methane (Moore 2001). Species of *Sphagnum* mosses have been claimed to contain more carbon in their living and dead tissues than any other genus of plants, including trees (Clymo and Hayward 1982). Peatlands are also important contributors in the water cycle. They provide freshwater storage and recharge surface and groundwater, can filter pollutants from water thereby providing surrounding lakes and rivers with a clean supply of freshwater (Rosenberg and Danks 1987). Owing to this ability, peatlands are sometimes employed in the treatment of wastewaters (Ronkanen and Kløve 2005).

Though peatlands are nutrient poor compared to other ecosystems, they support unique and diverse flora and fauna. Many organisms are believed to be restricted to these acidic environments and it has been noted that in comparison to other ecosystems, the proportion of peatland specialist species is high (Desrochers and van Duinen 2006). Plants commonly associated with peatlands include pitcher plants (*Sarracenia* spp.), butterworts (*Pinguicula* spp.), sundews (*Drosera* spp.) and a variety of ericaceous shrubs, which are able to survive in the nutrient-poor, acidic soils of bogs and fens, as they rely on insects for nutrients (Keys 1992). Peatlands serve as feeding and breeding sites for amphibians (Mazerolle 2001), waterfowl, shore birds (Desrochers and van Duinen 2006) and invertebrates (Spitzer and Danks 2006). While most mammals utilize peatlands for food or protection from predators, the southern bog lemming (*Synaptomys cooper* Baird) and the Arctic shrew (*Sorex arcticus* Kerr*)*, found in eastern Canadian peatlands, are among the only mammals thought to be bog specialists (Mazerolle et al. 2001). Despite the fact that peatlands support less diversity than other wetland classes, they serve as important habitats for many organisms, maintain unique biodiversity and have enormous research and education potential (Sanderson et al. 1993).

Anthropogenic threats to peatlands in Québec and Vermont

North American peatlands cover approximately 171 million ha of the territory; this translates to approximately 42% of the global peat area (O'Neill 2000). In Canada alone, peatlands cover 111 million ha, most of which is in boreal zone (Keys 1992). Between 7 and 9% of land area in Québec (approximately 12 million ha) is comprised of peatlands (Buteau 1988) and less than 1% of the state of Vermont (less than 25 thousand ha) is covered by these wetland ecosystems (Vermont Wetlands Office 2003). In Vermont and southern

Québec, peatlands often exist as isolated patches within an agricultural landscape and the health of these ecosystems can be impacted by significant changes in the adjacent landscape from human activity (Vermont Fish and Wildlife Department 2005). In this area, expanding industrial (hydroelectric industry, mining, forestry) and agricultural activities pose the greatest threat to peatland ecosystems (Poulin et al. 1999, Moore 2002) and approximately 210 000 ha of peatland have already been lost or damaged by human interference in Québec (Poulin et al. 2004).

The hydroelectric industry is the leading cause of peatland disturbance in Québec, where 120 000 ha have been flooded from damming. This activity mainly occurs in the northern boreal region of the province whereas other disturbances affect the more vulnerable peatland fragments of the highly populated southern portion of the province. It is estimated that in Québec, close to 11 000 ha of peatland have been lost to pastureland and farming of fruits and vegetables (Keys 1992, Parent 2001), though Poulin et al.(2004) postulate that this figure might actually be closer to 20 000 ha. In southern Québec, peatlands are often absorbed by farming activity in order to maximize land use; generally they are permanently altered as drainage, clearing and soil transformation are necessary processes to create an environment suitable for crops and grazing (Parent 2001). A growing sector of the agricultural industry in Québec is cranberry production. Peatlands (and the adjacent land) are ideal for these fruits, as they grow best in acidic environments with a pH between 4.0 and 5.5. Cranberry cultivation is harmful to peatlands as the land must be flooded to facilitate harvest (Parent 2001). In the last 20 years, drainage for forestry purposes has impacted almost 70 000 ha of peatlands in Québec (Parent 2000). Peatlands are seen as large expanses of relatively open land that could be used to increase silvicultural production, though the acidic and nutrient-poor state of the soil is not ideal for many tree species. To create an environment suitable for tree harvesting, the water table must be lowered by drainage. The upper peat layers then receive more aeration and nutrient uptake such that trees can grow and thrive (Macdonald and Yin 1999). A lesser threat to Canadian peatlands is the peat mining industry; the majority of Canadian operations are in Québec (Keys 1992) where in the southern region of the province peat is mined extensively (Pellerin and Lavoie 2003). There are currently 6 000 ha of peatlands in Québec used for the extraction of mainly horticultural peat (Poulin et al. 2004).

With the exception of large-scale disturbances from the hydroelectric industry, the 22 000 ha of peatlands in Vermont face similar threats as those in Québec (Malterer 1996). For example, the Molly Bog Peatland Complex in northern Vermont was described in the early 1970's as an "absolutely unspoiled cold northern bog" (US National Park Service 1973); less than three decades later it was declared 'threatened' due to logging, urban development, ditching and farming in and around the complex (US National Park Service 1989, Mouser et al. 2005). Many peatlands in Vermont are currently protected by organizations such as State of Vermont Department of Forests Parks and Recreation, the U.S. Fish and Wildlife Service and the University of Vermont. Likewise, in Québec, there are organizations such as ecological reserves, national and provincial parks with the purpose of protecting and conserving natural environments, including peatlands. The land within the boundaries of these areas is protected by provincial or national laws (Poulin and Pellerin 2001) as the intrinsic and ecological value of these lands is gaining attention from the public and scientific community.

Anthropogenic disturbance of peatlands has many potential ramifications. Ecosystems that perform important hydrological and biogeochemical functions for the environment are lost or permanently altered; vegetation and specialized plant species compositions are shifted and many animals lose important food sources and breeding grounds (Pellerin and Lavoie 2003). As interest in climate change and greenhouse gases grows, the large quantity of gaseous carbon contained within peatlands is receiving increasing attention (see Moore 2002). There is concern that human disturbance of peatlands, such as drainage, interferes with the hydrology of the ecosystem and the subsequent aerobic decomposition of the peat layer releases large amounts of carbon dioxide into the atmosphere (Moore 2001), though there is some dispute over the severity of this phenomenon (Moore 2002). Any anthropogenic disturbance to peatlands that alter their function and biotic communities could potentially have larger consequences for regional biodiversity (Lachance et al. 2005).

Peatland arthropod fauna

Arthropods may be the most abundant of all animals in peatlands (Spitzer and Danks 2006) and Finnamore (1994) estimates that there could be as many as 6000 arthropod species from just one Canadian fen. Though the arthropod fauna from European peatlands is better known (see Spitzer and Danks 2006), research on arthropods in Canadian peatlands is currently gaining momentum; however, taxonomic and life history information is still lacking for many species (Marshall and Blades 1989). While peatlands may superficially appear to be uniform habitats, there is in fact a great deal of internal heterogeneity and a variety of microhabitats that support a high diversity of aquatic and terrestrial arthropods. Ponds and natural pools (astatic and stable) that form in peatlands provide habitat and exclusive breeding ground for some arthropods (Larson and House 1990). Aquatic arthropods known from Canadian peatlands include Ephemeroptera and Trichoptera (Flannagan and Macdonald 1987), Odonata (Hilton 1987, Larson and House 1990), Hemiptera (Scudder 1987), Coleoptera (Larson 1987, Mazerolle et al. 2006) and Diptera (Lewis 1987, Rosenberg et al.1988); a number of species from these groups are thought to be peatland specialists but further study of life-histories will be necessary to support these observations.

Terrestrial arthropods found in peatlands are often generalist or vagrant species; they nonetheless contribute to the ecosystem functioning as do specialist species. Some species use peatlands in conjunction with the surrounding environments to complete their life cycle; for instance, Desrochers and van Duinen (2006) note that a species of the fruit fly genus *Tephritis* (Tephritidae) comes to peatlands when certain plants are flowering, sometimes even staying to overwinter. A wide variety of terrestrial arthropods have been collected from Canadian peatlands with abundant species belonging to the Hymenoptera, Diptera and Coleoptera (Blades and Marshall 1994). Among the groups of terrestrial arthropods thought to contain peatland specialists are spiders (Dondale and Redner 1994), odonates (Cannings and Cannings 1994), flies (Miller 1977, Marshall 1994, Dahlem and Naczi 2006) and to a lesser extent, beetles (Runtz and Peck 1994) and ants (Gotelli and Ellison 2002). Knowledge of the arthropod fauna that inhabit peatlands has greatly increased in recent decades but ecological studies focusing on arthropods in Canadian peatlands are lacking, despite the diversity and considerable ecological functions of these organisms.

Peatland Diptera

Diptera is one of the most species rich taxa found in peatlands. It is a highly diverse group, with both adult and immature stages displaying a wide variety of feeding habits. Flies are an integral part of a peatland ecosystem, occupying all trophic levels and acting as nutrient recyclers, primary and secondary consumers (Keiper et al. 2002) and providing a food source for several animals and carnivorous plants. Many Diptera families have been the focus of inventories from Holarctic peatlands, including the Sphaeroceridae (Marshall 1994, Roháček and Barták 1999), Dolichopodidae (Rampazzi 2002), Empididae (Barták and Roháček 1999), Chironomidae (Wrubleski 1987, Rosenberg et al. 1988), Tabanidae, Ceratopogonidae and Culicidae (Lewis 1987).

Despite their functional diversity, Diptera are rarely used in peatland ecology research, although a few recent studies have focused on the effects of disturbance on flies in Canadian peatlands. Blades and Marshall (1994) collected 522 species of flies from southern Ontario peatlands and found a greater proportion of non-peatland species were collected from a site modified by peat mining and drainage than from pristine sites. From one bog in southern Québec, Grégoire Taillefer et al. (unpublished data) collected 237 species of Schizophora and found diversity of flies from a trap adjacent to an abandoned drainage ditch to be lower than traps located deeper in the bog. Analyzing the 711 species of

Brachycera collected from three bogs in southern Québec, Grégoire Taillefer (2008) concluded that seven years of restoration efforts enhanced the recovery of Diptera diversity in three previously mined bog sections, though more time is required to restore the species compositions to those of natural bogs.

Diptera as peatland associates

The peatlands of southern Canada act as refugia for species that survived the Pleistocene glaciation (Marshall 1994) and certain Diptera species found in these isolated habitat fragments are thought to be disjunct populations from those in northern peatlands. Some Diptera species are considered characteristic of peatlands but also utilize other habitats. Other species have feeding and breeding constrained by the ecosystem properties of bogs and fens such that they are restricted to these environments. For example, in North America, the larvae of some species from the family Sarcophagidae use the decaying insects found in the peatland-restricted pitcher plant (*Sarracenia* spp.) as a food source (Dahlem and Naczi 2006). All eight species of the genus *Fletcherimyia* Townsend are associated with pitcher plants: *F. abdita* Pape, *F. celarata* (Aldrich), *F. folkertsi* Dahlem and Naczi, *F. jonesi* (Aldrich), *F. oreophilae* Dahlem and Naczi, *F. papei* Dahlem and Naczi, *F. rileyi* (Aldrich) *F. fletcheri* (Aldrich) as well as one species of the genus S*arcophaga* Meigen: *S. sarraceniae* Riley.

The peatland-inhabiting Sphaeroceridae from the Holarctic region have been well documented (Roháček 1984, Marshall 1994) in comparison to other Diptera families. There are 73 species of sphaerocerids known to inhabit Canadian bogs and fens; 15 are thought to be characteristic of peatlands (Marshall

1994). Three species of the genus *Pullimosina* Roháček are associated with peatlands: *P. (Dahlimosina) dahli* (Duda), *P. (Dahlimosina) bladesi* Marshall and *P. (Pullimosina) geminata* Marshall. There are six species in the genus *Spelobia* Spuler known to be connected to bogs and fens: *S. algida* Marshall, *S. acadiensis* Marshall, *S. bispina* Marshall, *S. ibrida* Roháček, *S. nana* (Rondani) and *S. pappi* Roháček. The genus *Ischiolepta* Lioy contains two species found in Canadian peatlands: *I. lama* Han and Marshall and *I. barberi* Han and Marshall. Two species in the genus *Phthitia* are peatland associates: *P. ovicercus* Marshall and *P. quadricercus* Marshall. *Pseudocollinella abhorrens* (Roháček) and *Pteremis wirthi* Marshall are the only species of these genera considered to be peatland associates. A single species in the family Lauxaniidae, *Homoneura (Tarsohomoneura) sheldoni* (Coquillett) is considered by Miller (1977) to be a species indicative of peatlands. There are undoubtedly more species of Diptera associated with peatlands than suggested by the literature; however, considering the large area peatlands cover in Canada, very few have been adequately sampled. Compounding the issue of inadequate sampling is the lack of taxonomic information and knowledge of the life-history traits of many Diptera groups.

Fragmentation and terrestrial islands

Habitat fragments are created after a large habitat area is reduced and divided into two or more isolated patches (Primack 2002, Johnson and Klemens 2005) mainly for the expansion of anthropogenic activities, such as urbanization and agriculture (Soule et al. 1990). These resulting remnants of land can be considered terrestrial islands, as their vegetation and species composition differ from the modified surrounding habitat. Habitat fragments can also be naturally occurring, resulting from natural processes like forest fires, intense wind storms, the action of river systems or geological processes. Peatlands can be considered natural terrestrial islands because flora and fauna are characteristic of these ecosystems and many species groups are restricted to these habitats (Moore 2002), especially in southern peatlands (Maltby 1986). Furthermore, the soil properties of peatlands contrast sharply with the surrounding environment and such habitats are considered 'islands of boreal diversity in a temperate zone', as many plant and animal species found further north are commonly found in temperate-zone peatlands (Calmé et al. 2002).

The biota inhabiting land remnants have been shown to be negatively impacted by landscape fragmentation, considered to be the leading factor in terrestrial biodiversity decline worldwide (Wilcox and Murphy 1985). The creation of remnant habitats affects ecosystem functions, population dynamics and reduces biodiversity in both the fragment and surrounding matrix (Saunders et al. 1991). As fragment size becomes smaller, the area-edge relationship decreases, so external factors are likely to exert a greater influence than internal factors on ecosystem dynamics. Larger fragments have bigger interior areas that are less affected by the different abiotic and biotic conditions associated with the edge, and often have greater habitat diversity compared with smaller patches (Saunders et al. 1991).

MacArthur and Wilson (1967) devised a model that relates the number of species on an island to the area of the island, known as the species-area relationship: $S= cA^z$, where S is the number of species on an island, A is the island area and *c* and *z* are constants that vary from system to system. This species-area relationship (SAR) applies in terrestrial islands created by habitat fragmentation where the creation of smaller habitat patches has led to a decrease in species richness of organisms such as plants (Cagnolo et al. 2006), lizards (Diaz et al. 2000), mammals (Bolger et al. 1997) and arthropods (Gonzalez 2000, Krauss et al. 2003). This reduction of species can largely be attributed to the decrease of suitable habitat, ecosystem degradation and increased difficulty of dispersal between isolated patches (Johnson and Klemens 2005). MacArthur and Wilson (1967) noted that their theory is not based on area *per se*, but on the idea that larger areas tend to support a broader range of habitats which in turn support more species. This caveat builds upon Williams' (1964) habitat diversity hypothesis which postulates that species richness may be a function of the number of habitats on a given island and the larger an island, the larger the number of habitats (Whittaker et al. 2007). In other words, as area of an island increases, the variability and heterogeneity of habitats increase, favoring higher species richness. In terrestrial islands, the habitat diversity hypothesis has been supported for peatland inhabiting birds (Stockwell 1994, Calmé and Desrochers 2000).

Insects are responsible for many crucial processes of ecosystem function and there is growing interest in examining the effects of habitat alterations on insect communities. Insects generally require narrower microhabitat conditions compared to vertebrates and examining their community fluctuations in response to disturbances can reveal valuable information on microhabitat changes (Deans et al. 2005). It is generally understood that insects are highly susceptible to the effects of habitat fragmentation (Kreuss and Tscharntke 1994, Gonzalez 2000, Kishbaugh and Yocom 2000); this could potentially interfere with their important ecological roles such as pollination, nutrient recycling and seed dispersal (Didham et al. 1996, Gibbs and Stanton 2001). Habitat fragments can be adversely affected by physical factors (see above) so it can be inferred that the biota in these remnant ecosystems are further threatened if the diversity of the local insect community decreases; however, this subject has yet to be adequately investigated (Didham et al. 1996, Gibb and Hochuli 2002).

Agriculturally-induced terrestrial fragments

As previously mentioned, urbanization and agriculture are the main causes of habitat fragmentation and are therefore the leading causes of habitat and species loss in Canada (Venter et al. 2006) and in the United States (Wilcove et al.1998). In the past sixty years, agriculture in Europe and North America has intensified (Krebs et al. 1999) so remnant forest patches have been further reduced and continually face further decimation. In southern Québec, the post-war era has seen a substantial shift from traditional farming to intensive agriculture practices resulting in increased wetland drainage and forest fragmentation (Jobin et al. 2003) such that less than 50% of the original forest cover remains in most counties in the region (Bélanger and Grenier 2002). The situation is more optimistic in Vermont, where approximately 80% of the state's land area is still covered by forest (Lubowski et al. 2002).

Within landscapes highly fragmented by agricultural practices, species richness in birds and small mammals has been shown to decrease (Nupp and Swihart 2000, Heikkinen et al. 2004). Similarly, increasingly intense agricultural practices also decreases species richness and alters community compositions in insects (Mazerolle and Hobson 2002, Schmidt and Tscharntke 2005, Hendrickx et al. 2007); the species richness of these communities inhabiting fragments adjacent to farm land can also be negatively affected by habitat area (Klein 1989, Denys and Tscharntke 2002). An overall decrease in habitat heterogeneity may be directing the decreased diversity in fragments as agriculturally associated species may dominate and outcompete other species. Commonly used fertilizers and pesticides may also negatively impact some organisms, leading to the observed decrease in species richness (Holland and Luff 2000).

Terrestrial habitat fragments are different than true oceanic islands as they are not completely isolated and the surrounding environment is not completely inhospitable for terrestrial species (Calmé and Desrochers 2000) so in addition to local habitat factors (such as vegetation and hydrology) the flow of vagile organisms is impacted by the composition and condition of the surrounding landscape (Ricklefs 1987, Yahner 1988). In other words, the type and degree of land use in a surrounding matrix may not only influence the species assemblages within a terrestrial island (Steffan-Dewenter et al. 2002) but also influence the species composition of the metacommunity. A metacommunity is defined as a group of local communities, within a region, from which multiple species can be exchanged by dispersal (Wilson 1992). Disturbance in the landscape may impact the diversity of a metacommunity by creating colonization opportunities and and altering competition and succession dynamics, thereby constraining the species composition within a habitat patch (Chesson and Huntly 1997, Platt and Connell 2003, Leibold et al. 2004). The condition of the matrix surrounding a terrestrial island may be so critical in structuring terrestrial arthropod metacommunities that local factors within the patch may be subordinate to greater landscape factors in determining species composition in arthropods (Schweiger et al. 2005)

OBJECTIVES

Landscapes are becoming increasingly fragmented and the resulting loss of habitat poses a serious threat to both peatlands and biodiversity in North America. No previous study has examined how habitat size and land use affect the species compositions of Diptera that inhabit peatlands in Canada or the US. Accordingly, the main objectives of this study are to 1) examine the effect of bog area on the species diversity of Schizophora fly assemblages that inhabit six temperate eastern Nearctic bogs by breaking down the concept of diversity into species richness, assemblage evenness and similarity and 2) to examine how vegetation structure within each site and the type and degree of land use practices in the surrounding landscape of the bogs influence the diversity and species compositions of Schizophora fly assemblages.

The group of focus in this study is Schizophora, a division of higher Diptera that include acalyptrate and calyptrate flies. The Schizophora include a variety of bog specialists, have high trophic and taxonomic diversity in peatlands and have previously been shown to be responsive to environmental perturbations in peatlands (Blades and Marshall 1994, Keiper et al. 2002, Dahlem and Naczi 2006, Grégoire Taillefer 2008) and so may be good indicators to use to examine the research objectives.

HYPOTHESES AND PREDICTIONS

Hypothesis 1: Bog area will have an effect on the species richness, evenness and similarity of Schizophora assemblages.

It has been shown that microhabitats in peatlands become more diverse as area increases resulting in positive SARs for certain taxa. This increase in microhabitats can be attributed to increased vegetation heterogeneity (Stockwell 1994, Calmé and Desrochers 2000). As many Diptera species directly interact with plants, I predict that as more microhabitats become available in larger bogs, more Diptera species will be present to fill the available niches. As heterogeneity increases with bog size and more Diptera species utilize the greater diversity of microhabitats available, I expect smaller and larger sites to become more similar in species compositions such that the assemblages of the small sites will be 'nested' within those of the larger sites. That is, there will be high species overlap between small and large sites. Larger habitat fragments are more resilient to influences from the surrounding habitats than are smaller fragments and I expect that as bog size increases, the species assemblages of Diptera will respond to this stability and have higher evenness.

Hypothesis 2: The degree and type of land use in the surrounding landscape and the vegetation structure of the bogs will have an impact on diversity and significantly influence Schizophora species compositions.

Many biodiversity studies in fragmented landscapes tend to focus only on habitat patches and ignore the influence of the surrounding matrix (Tscharntke et al. 2002), though it has been established that the quality and usage of the surrounding landscape affects both species compositions within terrestrial islands (Steffan-Dewenter et al. 2002) and ecosystem functions of wetlands (Burbridge 1994). Following these findings, I can predict that the degree and type of disturbance of the surrounding land will explain some variation in Schizophora compositions at each site. Furthermore, I expect the feeding habits of dominant species in an assemblage to reflect the type of disturbance in the landscape. For example, in those bogs where agricultural disturbance is prevalent in the landscape, I expect to find a dominance of certain groups generally associated with farming practices, for example, *Musca autumnalis* DeGeer, a species often associated with agricultural environments that was found in high abundance from a bog located in a region with intensive farming (J. Savage, pers. comm.). There is growing evidence that a feedback-loop exists between healthy, functioning ecosystems and diverse biotic communities (Naeem 2002, Hooper et al. 2005). From these findings, I expect that bogs with higher levels of pristine, undisturbed landscape will have more diverse assemblages.

Species composition of insects in peatlands is influenced not only by the species of plants present, but the structure of the vegetation and the microhabitats available (Lavoie 2001). In wetland ecosystems, certain groups of Diptera are closely tied to the species and density of vegetation present (de Szalay et al.1996, de Szalay and Resh 2000, Dahlem and Naczi 2006). In a bog ecosystem, a dominant presence of certain vegetation (e.g. trees) could impede the movement of flying arthropods, like Diptera, whereas a more open, *Sphagnum*-dominated system would allow more freedom of movement. Therefore, I can predict that differences in Diptera species compositions will be further explained by plant species and relative vegetation cover.

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CONNECTING STATEMENT

Temperate-zone peatlands act as terrestrial islands that are ecologically valuable but threatened by anthropogenic activities, as outlined in Chapter 1. Previous studies of North American peatlands have focused primarily on vegetation, birds, amphibians and mammals. Little attention has been given to flies, despite the fact that they are species rich, critical for a multitude of ecological processes within peatlands and are sensitive to environmental disturbance; these qualities make them ideal organisms to use for research on peatland ecology. Chapter 2 examines how peatland size and disturbance in the landscape affects species assemblages of Schizophora (Diptera) and discusses which environmental factors most influence their assemblage structure.

CHAPTER 2: EFFECTS OF HABITAT SIZE AND LAND USE ON DIVERSITY OF HIGHER DIPTERA IN TEMPERATE EASTERN NEARCTIC PEATLANDS

ABSTRACT

In southern Canada, peatlands are usually present as disjunct fragments, representing islands of northern boreal biodiversity in a temperate zone. These southern peatland fragments are particularly threatened by human disturbance. Although arthropods are abundant and ecologically diverse in peatlands and occupy all trophic levels, fundamental research on the diversity of terrestrial arthropods in bogs is incomplete and little is known about their response to habitat fragmentation and disturbance. Six bogs in southern Québec and northern Vermont, ranging in size from 12 to 900 hectares were sampled in the summer of 2006 to examine how bog size, vegetation and land use affects the species richness, evenness and species composition of Schizophora (Diptera) assemblages.. More than 6400 specimens, representing 381 species in 30 families were collected using Malaise traps, pan traps and sweeping. Bog vegetation structure and usage of the surrounding landscape up to 1500 m from the sampling location explained 66.7% of the variation in species composition and positively influenced Schizophora assemblages. Sites with intermediate levels of agriculture and forested land in the landscape had the most diverse assemblages. Bog size did not significantly influence Schizophora species richness, possibly due to the flow of species between the bogs and the surrounding landscape;two intermediate-sized sites had the highest diversity and evenness. Bog size did not explain the species

overlap between sites. Our results suggest that intermediate-sized bogs with moderate levels of agriculture in the landscape within a 1500 m radius around the site support diverse, healthy assemblages.

INTRODUCTION

Peatlands in the temperate zone of North America exist in a highly modified and populated landscape. In the past 200 years, it has been estimated that 20 million ha of peatlands have been lost in Canada alone (Environment Canada 1991). It is now estimated that 171 million ha of peatlands remain in North America (O'Neill 2000), with over 90% of these wetland ecosystems occurring in the boreal, subarctic and arctic regions (Malterer 1996, Tarnocai et al. 2005).

For many years, southern peatlands were regarded as 'wastelands' and drained for agricultural purposes, urban developments, mined for peat and used as landfill sites.However, it is now understood that peatlands contribute to the storage and cycling of water and carbon and provide habitats for many generalist and peatland-restricted plants and animals. In spite of peatlands' significant environmental roles, many temperate-zone peatlands still face pressure from anthropogenic interference which threatens to degrade the health of these precarious and valuable ecosystems.

Fragmentation from anthropogenic activities such as agriculture and urbanization is the leading cause of habitat and species loss in North America (Wilcove et al.1998, Venter et al. 2006). When a remnant habitat fragment has vegetation and a faunal species composition that differs from the modified landscape, it can be considered a terrestrial island; therefore, temperate-zone peatlands can be considered naturally-occurring terrestrial islands, as their soil properties and biota contrast sharply with the surrounding landscape. One way to examine the influence of the surrounding matrix on species inhabiting peatlands is to apply a hypothesis related to island biogeography (MacArthur and Wilson 1967), such as the species-area relationship (SAR): $S = cA^z$, where S is species richness, A represents the habitat area and c and z are constants. If peatlands do in fact act as islands, one could expect the species assemblages to conform to this theory, as shown for birds in peatlands from Québec (Calmé and Desrochers 2000) and Maine (Stockwell 1994). A positive SAR may not be a function of habitat area *per se*, but likely caused by the increase of microhabitats that result as habitat size becomes larger, leading to a higher number of niches available for more species; this effect is known as the habitat diversity hypothesis (Williams 1964). Terrestrial islands deviate from true oceanic islands in that they are not entirely isolated and are surrounded by habitat that is not completely inhospitable to terrestrial species. Therefore, a positive SAR may not entirely be a function of habitat area or number of microhabitats, but partially a function of the condition of the surrounding matrix and metacommunity dynamics resulting from the interactions between matrix and patch species.

While peatlands may act as terrestrial islands to a degree, there is no doubt that the surrounding landscape influences the flow of vagile organisms from the metacommunity. The composition and condition of the surrounding environment has been shown to influence species assemblages in habitat patches (Steffan-Dewenter et al. 2002) and in landscapes highly fragmented by agriculture, the species richness of birds, small mammals and insects was shown to decrease while their community compositions were altered (Nupp and Swihart 2000, Heikkinen et al. 2004, Schmidt and Tscharntke 2005). These trends could be the result of an overall decrease in habitat heterogeneity within the landscape created by fragmentation as disturbance may impact te diversity of a metacommunity by creating colonization opportunities and altering competition and succession dynamics (Chesson and Huntly 1997, Platt and Connell 2003). The condition of the matrixsurrounding a terrestrial island may be so critical in structuring terrestrial arthropods metacommunities that local factors within the patch may be subordinate to landscape factors (Schweiger et al. 2005).

There is high taxonomic and trophic diversity of arthropods in North American peatlands (Finnamore 1994, Keiper et al. 2002) and it has been suggested that arthropods are the most abundant of all animals in these wetland environments (Spitzer and Danks 2006). Insects are considered to be excellent indicators of an ecosystem's health because large sample sizes can be easily obtained, they occupy all trophic levels, have short generation times and can be sensitive to habitat changes (Kremen et al.1993, McGeoch 1998).

Despite the fact that insects represent about 60% of all described species (Grimaldi and Engel 2005) and perform a multitude of ecological roles, relatively few studies have focused on their responses to habitat fragmentation and landscape disturbance. It is generally understood that insect communities are susceptible to the effects of fragmentation (Gonzalez 2000, Kishbaugh and Yocom 2000) and agriculturally-induced disturbance (Mzerolle and Hobson 2002, Hendrickx et al. 2007), which could cause interference with their ecological functions such as pollination and nutrient cycling (Didham et al. 1996, Gibbs and Stanton 2001). Previous studies that have examined Diptera in disturbed Canadian peatlands focused on the effects of mining, drainage and restoration; the results showed that in those sites where the habitat was modified, species assemblages of

Diptera were negatively impacted compared to pristine sites (Blades and Marshall 1994, Grégoire Taillefer 2008, Grégoire Taillefer et al., unpublished data).

Given the magnitude to which the landscape in North America has been altered since the arrival of European settlers, is it fundamental to understand how species assemblages are affected by anthropogenic habitat fragmentation and various forms of land use. Therefore, the objectives of this research were to 1) examine the effect of habitat size on the species diversity of Schizophora (Diptera) assemblages that inhabit six temperate eastern Nearctic bogs and 2) to examine how the type and degree of land use practices in the surrounding landscape of the bogs and vegetation structure within each site influence the species compositions of Schizophora assemblages. The focal taxon in this study is the Schizophora, a division of higher Diptera that include acalyptrate and calyptrate flies. The Schizophora include a variety of bog specialists, have high trophic and taxonomic diversity in peatlands and have previously been shown to be responsive to environmental perturbations in peatlands (Blades and Marshall 1994, Keiper et al. 2002, Dahlem and Naczi 2006, Grégoire Taillefer 2008).

MATERIALS AND METHODS

Site descriptions

The study sites were six ombrotrophic bogs located in southeastern Québec and northern Vermont (Fig. 2.1), a heavily populated region with highly transformed landscapes. All sites were located within the temperate deciduous forest region of North America and the dominant vegetation across all sites was ericaceous shrubs and *Sphagnum* spp. mosses. Selection of sites was based on bog size which ranged from 12 ha to 900 ha and the degree of various land uses in the surrounding region. Distance between sites ranged from 48 km to 303 km.

Marlington Bog

Marlington Bog (MAR) (45^{o}02.4'N, 72^{o}10.4'W) is a peatland of 12 ha located in Stanstead, Memphrémagog County, Québec. It is currently a protected site and is managed by the Nature Conservancy of Canada. The site is immediately surrounded on all sides by pristine deciduous forest and the local landscape, up to 2 km from the site, mainly consists of an equal mix of forest and agricultural fields. The peatland is in a generally circular shape.

Lake Carmi Bog

Lake Carmi Bog (CAR) (44 ^{o}57.2'N, 72 ^{o}52.9'W), located in Lake Carmi State Park, Franklin County, Vermont, is a protected bog with an area of 57 ha. The bog is directly surrounded by deciduous forest and there are a few small campsites along the north edge. Lake Carmi, a freshwater lake with a surface area of 556 ha, is located 75 m north of the bog. The land surrounding the bog, up to 2 km away, is dominated by agricultural fields and to a lesser extent, forest and fresh water, from the lake. The bog at Lake Carmi is heart-shaped.

Johnville Bog

Johnville Bog (JON) (45 °59.8’N, 73 °18.0’W), located in Johnville, Haut-Saint-Francois County, Québec, has an area of 60 ha. The protected peatland is part of the Johnville Bog and Forest Park and managed by the Johnville Woodland Conservation Corporation. There is undisturbed forest surrounding the majority of the bog except for an abandoned agricultural field bordering the northeast edge. Agriculture is the dominant land use practice in the landscape, up to 2 km from the bog site, followed by forested and urban land. The shape of this peatland is oblong and irregularly shaped, with pockets of peatland jutting into the surrounding forest.

Frontenac Bog

Frontenac Bog (FRN) (45 °58.1’N, 71 °09.1’W) is a protected site of 150 ha located in the Parc national de Frontenac, l’Amiante County, Québec. The bog, up to 2 km around, is surrounded by pristine deciduous forest that is protected by the MDDEP (Ministère du Développement durable, de l’Environnement et des Parcs) of Québec. Frontenac Bog is generally circular in shape.

Réserve écologique des tourbières-de-Lanoraie

The Réserve écologique des tourbières-de-Lanoraie (LAN) (45 °59.8’N, 73 °18.0’W), d’Autray County, Québec, has an area of 415 ha. The study site is part of a parcel of land, protected by the MDDEP, that sits in a larger, highly-fragmented peatland complex .The reserve is surrounded minimally on all sides by unprotected peatland, and agricultural fields and forested land are the major land use types up to 2 km from the site. The shape of the protected portion of the peatland is irregular and amoeba-like, with pockets of forested land jutting inward.

Large Teafield

The Large Teafield (BAR) (45 °07.5'N, 74 °13.5'W) is a bog of 900 ha located in Sainte-Barbe, Haut-Saint-Laurent County, Québec. The site is currently unprotected and privately owned. The land surrounding the bog, up to 2 km from the site, is dominated by intensive agriculture and the entire bog is bordered by agricultural fields. The peatland is generally rectangular-shaped.

Sampling and Specimen Preparation

Sampling took place from 12 June to 26 July 2006 using a combination of pan traps, Malaise traps and net sweeping, following the recommendation of Marshall et al. (1994) to use multiple sampling techniques in order to collect a diverse representation of flies with various life-histories and behaviors The pan trap design in each of the six bog sites consisted of three parallel transects of four pan traps. The first trap of each transect was placed approximately 5 m from the bog edge. Each transect was spaced ten meters apart and each pan trap within a transect was also spaced ten meters apart. The pan traps consisted of yellow plastic bowls 4.5 cm deep and 12.5 cm in diameter placed in the substrate with the upper rim flush with the ground. A solution consisting of equal parts propylene glycol and soapy water (to break surface tension) was used as a preservative. A Malaise trap was installed approximately 40 m from the bog edge at each site for seven days, every second week. Flies were also sampled by doing 80 sweeps of vegetation using a sweep net in the area near the Malaise trap. Sweeping and trap servicing were done every seven days.

Flies from pan traps and sweeping were preserved in 70% ethanol; flies caught in Malaise traps were preserved in 95% ethanol to preserve genetic material for other studies. Large flies were pinned and air-dried from alcohol; small flies were chemically dried using hexamethyldisilazane (HMDS). All specimens of Schizophora, excluding Anthomyiidae, were identified to species when possible or morphospecies if taxonomic keys were unavailable. Voucher specimens were desposited at the Lyman Entomological Museum (Sainte-Anne-de-Bellevue, Québec).

Land use variables

To determine how land use in the matrix surrounding each bog site affects Schizophora diversity, orthophotos (aerial photographs that have been corrected for distance distortion) of each site were analyzed using ArcMap 9.2 software (ESRI 2006). Orthophotos of 1:50 000 for JON, FRN, LAN and BAR were obtained from Canadian Minister of Natural Resources CanImage series; a 1:40 000 orthophoto of MAR was obtained from the Photocartothèque Québécoise and a 1:4000 orthophoto of CAR was obtained from the Vermont Mapping Program. Land use around each site could easily be distinguished in all photos regardless of resolution. Concentric rings with radii of 500, 1000, 1500 and 2000 meters were buffered around the sampling location at each site to examine the percent land use of the following categories: forest, agriculture, peatland, open water and urban.

Maximum flight distance of flies is difficult to measure, though Kurahashi (1991) noted that certain species from the family Calliphoridae are capable of flying hundred of kilometers (see Johnson 1969 for other examples). However, in these instances, strong air currents could be responsible for propagating the insects farther than they would fly under normal circumstances. Hence, these distances are likely extreme values and are not necessarily accurate representations of their average flight ranges. Other studies involving both acalyptrate and calyptrate Diptera suggest that flies in these groups generally have a dispersal range under two kilometers (Finch and Collier 2004, Meats and Smallridge 2007, but see Johnson 1969 and Stein 1986). Based on these estimates, a maximum buffer distance of 2 km around each site was selected to encompass the typical flight range of Schizophora flies.

Vegetation variables

Percent vegetation cover was estimated on 16 and 17 July 2007. It is unlikely that the cover or species composition of the vegetation had significantly changed from the previous year, as the low nutrient state of a bog ecosystem leads to low productivity and a slow growth rate of plants (Gunnarsson et al. 2000). Percent vegetation cover was estimated in twelve quadrats of 1m x 1m in each site. These values were averaged across each site. The vegetation strata estimated included: ericaceous shrubs, grasses, *Sphagnum* mosses, other mosses, herbs, litter, lichen, trees and ferns. The areal cover method was used to estimate actual (i.e. total) percent vegetation cover per quadrat and this value sometimes exceeded 100%, as there was overlap in the strata (Tiner 1999).

Data Analyses

Species diversity and composition of Schizophora

The first objective was analyzed by breaking down the concept of diversity into species richness (α-diversity) and species overlap (ß-diversity). As raw species richness is sensitive to sample size, it is not the most advantageous measure of diversity (Buddle et al. 2005). Therefore, the species richness at each site was estimated using individual-based rarefaction which retains power even when sampling effort between sites is varied and accounts for missing or disturbed traps (Gotelli and Colwell 2001). Rarefaction allows for comparisons of species richness between sites when samples are standardized to the abundance of the least abundant sample, then repeatedly subsampled by Monte-Carlo simulations. The generated curves also provide estimates of variance for statistical comparisons of species richness between sites and can determine whether sampling effort was adequate. Rarefactions were performed using EcoSim version 7.58 (Gotelli and Entsminger 2003).

The intrapolated species richness estimate obtained by rarefaction was compared to an extrapolated estimate from the abundance-based coverage estimator (ACE). ACE is a non-parametric measure that uses the assumption that highly abundant species cannot aide in predicting the actual richness of the assemblage (Magurran 2004). By emphasizing those species represented by one to ten individuals, ACE can approximate how many species per site may be present but not sampled. This method is a preferred estimator of species richness as other measures that use singleton and doubleton information (e.g. Chao 1) tend to overestimate richness (Magurran 2004). ACE estimates were computed using EstimateS version 7.5 (Colwell 2005).

The diversity of Diptera assemblages at each site was ranked using the Simpson diversity index (Simpson 1949). This measure is based on species abundance and is weighted heavily on those species which are most abundant. The reciprocal form of the measure was used in this study as the value of the measure increases as the assemblages become more even, so is more intuitive than other forms of the index (Magurran 2004). A low value indicates low relative diversity, indicating that one or two species dominate and the assemblage has low evenness (Magurran 2004). To obtain a visual representation of the relative evenness the species assemblages, rank-abundance curves were used for 15 of the most commonly collected Schizophora species fromall sites after pooling..

Differences in species compositions between sites were analyzed using the Bray-Curtis index (a.k.a. Sørensen quantitative index), which evaluates distinctness of assemblages. This nonmetric estimator is based on the relative abundance of species, so a dominant species carries more weight than a singleton, but is less sensitive to the abundance of the most abundant species than other nonmetric similarity indices (e.g. Morisita-Horn index) (Magurran 2004). Pairwise comparisons between all sites were performed to assess similarity. The Bray-Curtis index was computed using EstimateS version 7.5 (Colwell 2005).

Species compositions between sites were compared using nonmetric multidimensional scaling (NMDS) ordination, a non-parametric tool that aims to reduce the dimensionality of the data while graphically plotting similar data points (e.g. traps, sites) close together and dissimilar points further apart in ordination space (Legendre and Legendre 1998). This method makes no *a priori* assumptions of spatial relationships among variables (McCune and Grace 2002). Individual traps were separated and pooled across the sampling period, singletons and doubletons were removed and species abundance data were log-transformed ($x' = \log(x + 1)$) prior to analysis. A detrended correspondence analysis (DCA) ordination was used for the starting configuration to reduce stress levels and avoid local minima (Work and McCullough 2000). A preliminary six-dimensional NMDS ordination was first run to determine the number of recommended dimensions; the final ordination was then performed using the suggested number of axes. Parameters including the Bray-Curtis distance measure, 50 runs with real data, 100 runs with randomized data and a Monte Carlo test of significance were used for all ordinations. NMDS ordinations were conducted using PC-ORD version 4.36 (McCune and Mefford 2005).

Indicator species analysis (Dufrêne and Legendre 1997) was used to examine species-sites affinities using PC-ORD version 4.36 (McCune and Mefford 2005). Statistical significance was tested with a Monte Carlo test of 1000 runs for indicator values. Species with indicator values greater than 25 combined with a significant p-value (<0.05) were considered as site indicators.

Schizophora responses to habitat size

A linear regression was performed using Excel (Microsoft Office Excel 2003) to determine the relationship between species richness and site size. The species richness estimates obtained from ACE were used and size data were log-transformed (x'= log(x)) prior to analysis to reduce the effect of the smallest and largest sites.

Schizophora responses to environmental variables

Percent land-use categories outlined above (at 500, 1000, 1500 and 2000 m from sampling location) and percent vegetation cover from each site were condensed using five individual Principal Components analyses (PCA). PCA is an ordination method that reduces original variables into uncorrelated, independent variables which capture as much variation as possible from the data (Gotelli and Ellison 2004). In subsequent analyses, the first axis score from each PCA of land use were then used as independent variables called Land500, Land 1000, Land1500 and Land2000. The first two axes scores from the PCA of vegetation cover were used as independent variables in subsequent analyses and called Veg1 and Veg2. Eigenvector coefficients obtained from PCA indicate which of the original variables carry the most weight within the condensed variable (McGarigal et al. 2000). The independent variables were decomposed, showing the eigenvectors with the highest values.

Canonical Correspondence Analysis (CCA) was performed for each category of variable. CCA is a type of ordination that relates major gradients in species data to measured explanatory environmental variables (McGarigal et al.

2000). A preliminary CCA was performed using the land use variables and Land2000 was not shown to impact species compositions and was thus omitted from subsequent analyses. A second CCA was performed using the Veg1 and three remaining land use variables to determine the influence of the environmental variables on the species assemblages. Log-transformed ($x' = \log (x + 1)$) species abundance data with singletons and doubletons omitted were used for both PCA and CCA. Monte Carlo tests of 500 runs were used to test significance of the axes with the null hypothesis that there is no relationship between the species assemblages and environmental variables. Both the PCA and CCA were performed with PC-ORD version 4.36 (McCune and Mefford 2005).

RESULTS

A total of 6470 specimens of Schizophora, representing 381 species in 30 families was collected (Appendix 2.1). The most species rich families were: Tachinidae (73 species), Muscidae (70 species), Chloropidae (40 species), Sarcophagidae (24 species) and Sphaeroceridae (22 species). The most individuals were collected from JON and lowest number of individuals was collected from CAR (Table 2.1). In terms of raw species richness, the highest number of species species was found from JON and fewest were collected from CAR (Table 2.1). One hundred fifteen species were represented by one individual (singletons) and sixty-five species were represented by two individuals (doubletons).

Schizophora assemblage and composition characteristics

The curves generated by rarefaction did not reach an asymptote (Fig 2.2), suggesting that sampling of Schizophora species was incomplete at all sites. This result supports the findings obtained from the ACE estimate of species richness, which found that between 31 and 49% of Schizophora species at the sites were not collected (Table 2.1). The rarefaction estimate of species richness indicates that the species richness of all sites was significantly different from one another except at MAR and FRN, where the standard deviations of species richness overlapped (Table 2.1). Rarefaction ranked LAN as the most species rich site, followed by (in order of decreasing richness): JON, CAR, FRN, MAR and BAR (Table 2.1). Simpson's diversity index ranked the two smallest sites, MAR and CAR, as having the least diverse assemblages, implying that one or two abundant species dominated these assemblages. The two most diverse sites were JON and LAN (Table 2.1). Rank abundance curves (Fig 2.3) were generated to show changes in species assemblage evenness across sites.

According to the Bray-Curtis index, MAR and FRN and MAR and BAR had the highest species-overlap and can therefore be considered the most similar sites. The least similar sites were MAR and LAN and FRN and LAN (Table 2.2). The NMDS ordination explained 69.3% of the variation in three axes. Axis 1 and axis 2 explained the most variance with 25.3 and 22.3%, respectively and are graphed in Fig. 2.4. There was clustering of the species assemblages by site though there was a lot of overlap between certain assemblages, especially between MAR and FRN; this supports the results from the Bray-Curtis index. The assemblage from BAR appeared to be the most distinct. Species assemblages did not cluster by site size along either axis 1 or 2 (Fig. 2.4). The stress value of the ordination was 18.506. Indicator species analysis revealed twenty-five Diptera species positively associated with the six sampled bogs. Ten species were associated with BAR, eight with JON, five with LAN and one each with MAR, CAR and FRN (Table 2.3).

Schizophora responses to habitat size

A weak, non-significant relationship between bog area and Schizophora species richness was found by the linear regression. Bog area accounted for 21.2% of the variation in Schizophora species richness ($p>0.05$, Fig. 2.5), suggesting that other variables are influencing the number of species at the sites.

Schizophora responses to environmental variables

The first axes of the three reduced land use variables obtained from PCA, Land500, Land1000 and Land1500, explained 49.9, 48.5 and 41.9% of the variance in the species data, respectively. The variables that carry the most weight from each condensed land use variable are: forest, peatland and arable land for Land500; forest, peatland and arable land for Land1000 and peatland, urban and forest for Land1500 (Fig 2.6). The first two axes of the reduced vegetation variables explained 73.6% of the variation in species data. The variables that carry the most weight from the condensed vegetation variables are: *Sphagnum* spp., grass, ericaceous shrubs and litter for Veg1 and herbaceous plants, ferns, trees and lichens for Veg2.

In three canonical axes, the CCA explained 69% of the variation in Schizophora species composition (Fig 2.6). The percentages of variance accounted for by the three axes are 28.5, 22.1 and 18.4%, respectively. The first canonical axis was signifcant according to the Monte Carlo test (p= 0.004). Land1000 and Land1500 were positively correlated with axis 1, Veg 2 was negatively correlated with axis 1 and both Land500 and Veg1 were positively correlated with axis 2 (Table 2.4). Species assemblages in those sites on the positive side of axis 1 (MAR, JON and FRN) appeared to be influenced by a high cover of *Sphagnum* spp., high forest cover and low peatland and arable land cover in the landscape up to 1500 m around the site. The site on the negative side of axis 1 and 2 (BAR) appeared positively associated with site area and high peatland and arable land cover and low forest cover up to 1500 m around the site. This site also seemed positively influenced by high cover of ericaceous shrubs and low cover of *Sphagnum* spp.

DISCUSSION

The objectives of this study were to examine the effect of habitat size and the influence of surrounding land use and within-site vegetation cover on Schizophora species assemblages in eastern Nearctic peatlands. The results indicate that bog size had no effect on the species richness, evenness or overlap of Schizophora assemblages. Vegetation cover and the condition of the surrounding landscape explained a high proportion of the variation in the species assemblages and greatly influenced Schizophora species compositions and diversity at each site.

Schizophora responses to environmental variables

Effects of land use and in-site vegetation on species compositions

Previous studies have suggested that local habitat factors may be subordinate to landscape factors in determining arthropod species compositions (Schweiger et al. 2005). However, the results of this study show that both local, in-site vegetation and landscape conditions were significant determinants of Schizophora species compositions. Flies of the metacommunity (here defined as the community of Diptera inhabiting the sampled bogs and the land up to 2 km around the sites) were influenced by the specific land uses in the habitat matrices. The inclusion of surrounding matrix effects in ecological studies of arthropods in fragmented landscapes has long been ignored but is gaining momentum (Krauss et al. 2003, Steffan-Dewenter 2003, Lövei et al. 2006). To my knowledge, no previous study has focused on how surrounding land use affects arthropods in peatlands. The condition of the landscape and bog vegetation composition create site-level differences that would affect the species compositions of flies, as the feeding and breeding habits of some species depend on particular plants and substrate (e.g. decaying organic matter) to complete their life cycles. The total variability in species composition data explained by the environmental factors fell within the range generally achievable with CCA (Økland and Eilertsen 1994) and showed that, as expected, different land-use practices and vegetation composition and cover significantly influenced the species composition of Schizophora assemblages in the six sampled bogs.

The results of the CCA highlight the importance of landscape quality and habitat diversity in a region where anthropogenic disturbance has greatly modified the landscape. Not all sectors in southern Québec and northern Vermont had similar levels of forested land (US Forest Service 1997, Bélanger et al.1999) and this was reflected in the Schizophora species compositions. A notable example was BAR, which had the most direct agricultural disturbance, with fields and pastures bordering every edge of the bog; the other sampled bogs were less directly disturbed by agricultural activities. BAR was the only site where the species composition was positively associated with a low forest cover and high cover of arable land up to 1500 m from the sampling point. This result emphasizes that even a narrow buffer zone of forested land between a bog and farmland, as was present at the other sites, can at least partially direct species compositions. The effects of buffer zones around the bog sites were not specifically tested in this study, though zones between 1-2 km have previously been recommended to protect wetland biodiversity (Findlay and Houlahan 1997).

A species-site association could imply the presence of environmental conditions suitable to the indicator species or the presence of another organism the indicator species preys upon (du Bus de Warnaffe and Dufrêne 2004). As predicted, several species were found to be indicative of specific vegetation or land use type at the bog sites. Larvae of *Minettia lupulina* Fabricius (Lauxaniidae) are known to mine decaying leaves of Sugar Maple (*Acer saccharum* Marshall), Wild Cherry (*Prunus serotina* Ehrhart) and Black Spruce (*Picea mariana* (Miller)) trees. This species was associated with BAR, where plant litter positively and significantly influenced species compositions. One of the dominant tree species in the Upper Saint Lawrence River municipality is Sugar Maple (Jean and Bouchard 1986), so it is likely that *M. lupulina* was feeding on the rotting leaves of this tree. Two species from the family Muscidae were found to be indicator species of JON: *Eudasyphora cyanicolor* Loew and *Musca domestica* Linnaeus; another species, *Musca autumnalis* DeGeer had a relatively high abundance from JON but did not come out as an indicator species of the site. These species are commonly found near agricultural activity and are known to breed in manure heaps (Ferrar 1987). Though the results indicated that the species assemblage from JON was not influenced by high cover of arable land in the landscape, it is worth noting that a large proportion of the surrounding habitat was comprised of agricultural lands andthe high abundance of these species from this site indicates they specifically were associated with nearby agricultural practices.

Effects of land use on diversity

My findings did not support my prediction that those bogs surrounded by high levels of pristine land would have the most diverse Schizophora assemblages. The bog which had no anthropogenic disturbance in the landscape within a 1500 m radius, FRN, was ranked as intermediately diverse compared to the other sites which were disturbed by agriculture and urbanization. Habitat disturbance is considered to be a very important determinant of arthropod community composition (Spitzer et al. 1993). There is a widely supported view that the variety of microhabitats and vegetation structure created after a disturbance to a forested habitat support a higher species diversity than an undisturbed forest system (Spitzer et al. 1993, Spitzer et al. 1997, Hamer et al. 1997) as disturbances can shift patch resource levels that contrast with the surrounding undisturbed habitat (Huston 1994). Disturbance alters the dynamics of a community and the resulting successional stages of the vegetation create a distinct resource environment for the metacommunity (Questad and Foster 2007).

This idea can be related to this study as all bog sites currently are, or were, surrounded by forest that has been since modified by anthropogenic interference. The Intermediate Disturbance Hypothesis (IDH) (Connell 1978) is a theory that predicts species diversity patterns under different levels of habitat disturbance and asserts that higheest diversity occurs where a habitat is disturbed at intermediate frequency or intensity. This theory has explained the diversity patterns for multiple wetland arthropod taxa (Ward and Stanford 1983, Townsend 1997, Whiles and Goldowitz 2001). The IDH provides a possible explanation for the high diversity of the species assemblages from LAN and JON. Compared to BAR (very disturbed matrix) and FRN (very pristine matrix), LAN and JON are moderately disturbed by agricultural practices and urban development (JON only) up to 1500 m from the sampling location. Otherwise, the sites are surrounded by forested land, peatland or water (JON only). The pristine ecological conditions provided by the intact forest and peatland combined with the agricultural fields and associated farming practices (e.g. livestock) potentially created many microhabitats such that a high number of species were able to colonize the area.

An alternative explanation for the high diversity from LAN and JON relates to a possible interaction between the IDH and bog shape. An often-overlooked attribute of terrestrial fragments is shape complexity (Ewers and Didham 2006). At the most basic level, shape is defined by the perimeter-habitat core relationship (Laurance and Yensen 1991) so long, narrow fragments and increased shape complexity increases the proportion of edge and reduces the amount of core habitat. Therefore, rectangular and complex-shaped patches are more exposed to the surrounding habitat and any disturbance that may be present. Among the bogs sampled in this study, LAN and JON were the most complex in shape, being both long and narrow, with forest pockets jutting in from the matrix. Consequently, LAN and JON are the most diverse bogs sampled owing to their shape and resulting increased exposure to the intermediately-disturbed conditions of the habitat matrix (as outlined above).

Schizophora responses to habitat size

Contrary to the prediction that a significantly positive SAR would exist between bog size and the number of Schizophora species, habitat size did not significantly affect the species richness of flies likely due to the movement of flies from the metacommunity The positive association between insect species richness and terrestrial fragments is a well-documented pattern (Krauss et al. 2003, Steffan-Dewenter 2003, Martinko et al. 2005, Ouin et al. 2006) though Bolger et al. (2000) found no correlation between habitat fragment size and species richness of bees and wasps. Vegetation heterogeneity likely increased with larger bogs, as shown by other studies (Stockwell 1994, Calmé and Desrochers 2000) and the lack of effect of increasing size (and increasing number of microhabitats) on species richness indicates that the habitat diversity hypothesis is not applicable to my results. The absence of a significant SAR can be attributed to the movement of flies between the bogs and the surrounding habitat matrix and any possible size effects may have been confounded by this exchange of speciesIt has been postulated that the SAR is stronger for habitat specialists than for generalists (Harrison and Bruna 1999). This relationship could possibly exist for dipteran bog specialists, however, there is currently not enough knowledge of peatland Diptera to properly assess this theory.

The high evenness that characterized the species assemblage from LAN, the second-largest site, followed the prediction that assemblages from larger sites would have higher evenness than smaller sites. However, the Schizophora assemblage from the largest site, BAR, had relatively low evenness. The two smallest sites, MAR and CAR, were characterized as having the lowest evenness and diversity, according to the Simpson index. The low evenness and diversity of these two small bogs can perhaps be attributed to the dominance of *Paramyia nitens* (Loew), a small species of saprophagous Milichiidae. It is possible that feeding conditions at MAR and CAR were favorable to *P. nitens* such that it outcompeted other saprophagous taxa and dominated that trophic group. An alternative explanation for the low Schizophora diversity of MAR relates to the small size of the site and the high cover of forest in the surrounding matrix. The ecosystem dynamics are progressively more influenced by external factors as the amount of core habitat decreases, as is the case with small terrestrial fragments (Saunders et al. 1991). Open bogs have been found to have higher insect species richness than forested bogs (Spitzer et al. 1999, Lavoie 2001) so the high forest cover of the land surrounding MAR may have masked the presence of the small bog. Additionally, the heavily forested area may have acted as a dispersal barrier for species of flies (Moertelmaier 1996) that are not able to cross through dense tree cover. Consequently, in terms of species composition of flies, MAR may act more like a forest than a bog.

The NMDS ordination did not show a clear differentiation of species compositions based on bog size. Assemblages were placed close together in ordination space, indicating that they were, overall, relatively similar to one another. Individual species assemblages were slightly grouped at the site level, though there was a lot of overlap between them, as supported by the analysis of similarity. The Bray-Curtis index showed MAR as being most similar to FRN, an intermediate-sized bog and BAR, the largest bog. These results suggested that the assemblage from the smallest site is possibly nested in the assemblages of the larger sites, as was expected. However, this trend was not observed for MAR and FRN which were found to be least similar to the species assemblage from LAN, the second-largest site. This last result can likely be attributed to variation in vegetation structure and landscape condition between the sites, which were shown to significantly influence the Schizophora species assemblages at the six sampled bogs.

Scale of study

The high amount of variation in the species data explained by environmental variables may be the result of the large spatial-scale at which they were measured. Variables measured at the landscape scale have been shown to have more impact on arthropod assemblages than when measured at the local scale (Økland et al. 1996, Schweiger et al. 2005). Furthermore, other landscape studies have suggested that the scale at which landscape condition and use affects species depends on their foraging or dispersal distances (Keitt et al. 1997). For example, tropical moth assemblages in an agricultural landscape were most affected by cover of forested land within a 1000 and 1400 m radius (Ricketts et al. 2001) and honeybee species dynamics were influenced by landscape condition in 3000 m radius (Steffan-Dewenter et al 2002). Though there is some dispute as to general dispersal distances of flies (see Land Use Variables section), the results of this study indicate that land use within a 1500 m radius around a bog is enough to significantly influence Schizophora species composition.

Sampling issues with Diptera

The high number of species collected from this study support previous findings that flies are species rich and diverse in bogs, even though the rarefaction and ACE results suggested that many species were not collected from the study sites. Other authors have noted the difficulty in obtaining complete samples of a Diptera assemblage from a particular study location. For example, 15 years of continuous operation of one Malaise trap was not considered adequate time to completely sample the species of a diverse genus from the family Phoridae in the tropics (Brown and Feener 1995). Owen (1981) operated a Malaise trap continuously for seven months a year, over eight years and estimated that only 67% of Syrphidae species known from the study region were collected. Many biodiversity studies tend to have a shorter duration than the aforementioned studies and are unable to sample a Diptera assemblage to completion. However, obtaining representative samples increases knowledge and understanding of the diversity in the sampled region and researchers should use multiple trapping techniques in order to collect the most diverse sample possible.

Conservation and management implications

The myriad values of peatlands have been acknowledged through various wetlands conservation policies at the provincial and state level (Ministère de l'environnement 2000, Vermont Wetlands Office 2003), national level (Environment Canada 1991) and even the continental level, with the North American Wetlands Conservation Act (US Fish and Wildlife Service 2008). These regulations were created to preserve and sustain the ecological and socio-economic functions of all types of wetlands. Despite these multi-tiered policies, Québec's peatlands are under-protected, especially given the large area they cover. Presently, less than 1% of Québec's peatlands are protected (Poulin and Pellerin 2001). The status of peatland protection in Vermont is far more optimistic, where it has been estimated that approximately 87% of peatlands exist on protected land, though future inventories will likely refine this number (E. Sorenson, pers. comm.).

The Diptera assemblages analyzed in this study reflected the measured environmental variables and future management decisions based on anthropogenic impacts to peatland diversity should likewise focus on biotic indicators that are sensitive to environmental disturbance (Cairns et al. 1993). For example, Findlay and Houlahan (1997) concluded that amphibians, reptiles and mammals were more useful than birds when detecting trends of human impacts on wetland biodiversity. Studies focusing on anthropogenic impacts on peatland communities are only recently gaining momentum (Mazerolle and Cormier 2003, Deans et al. 2005, Mazerolle et al. 2006, Grégoire Taillefer 2008) so relatively little information exists about human-mediated affects on peatland diversity. From this study, it can be recommended that future peatland conservation policies focus on preserving remaining surrounding forest and creating a balance between agricultural activity and pristine land to maintain diverse Diptera assemblages. Further investigations into the mechanisms that affect peatland diversity will be necessary to provide more insight into conservation and management strategies.

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Table 2.1: Observed species richness (S_{obs}), overall abundance (n), rarefaction estimates of species richness (richness ± 1 SD, standardized at 439 individuals), ACE estimates of spcies richness and Simpson's diversity index of Schizophora species listed by bog site.

Site	S_{obs}	**n**	**Rarefaction**	**ACE**	**Simpson's**
MAR	145	1164	88.72 ± 4.57	210.1	3.11
CAR	95	439	95.00 ± 0.0	183.4	6.50
JON	182	1537	101.09 ± 5.06	298.42	15.00
FRN	151	1298	89.69 ± 4.70	259.47	9.29
LAN	124	530	111.61 ± 2.93	241.3	33.82
BAR	146	1502	79.04 ± 4.84	276.78	8.10

Table 2.2: Pairwise site comparisons with corresponding Bray-Curtis value. Larger values indicate more similarity between sites. * indicates pairs of sites with highest similarity; ** indicates pairs of sites with lowest similarity.

	BAR	LAN	FRN	JON	CAR
MAR	0.474*	0.201**	0.476*	0.414	0.388
CAR	0.283	0.247	0.337	0.341	
JON	0.346	0.221	0.435		
FRN	0.375	0.183**			
LAN	0.207				

Table 2.3: Indicator species analysis of Schizophora species from all study sites. Only species with indicator values (I.V.) of >25.0 and significant p-values (p<0.05) are included.

Family	Species	Site	I.V.	p-value
Chloropidae	*Thaumatomyia pulla*	JON	34.3	0.002
Drosophilidae	*Drosophila sp. iii*	LAN	36.1	0.001
Drosophilidae	*Drosophila sp. iv*	BAR	35.0	0.001
Ephydridae	*Notiphila (Dichaeta) caudata*	LAN	32.7	0.011
Ephydridae	*Scatella (Scatella) stagnalis*	BAR	37.6	0.001
Lauxaniidae	*Homoneura (Tarsohomoneura) sheldoni*	JON	65.2	0.001
Lauxaniidae	*Minettia lupulina*	BAR	39.6	0.001
Muscidae	*Eudasyphora cyanicolor*	JON	29.4	0.019
Muscidae	*Musca domestica*	JON	25.8	0.045
Muscidae	*Muscina assimilis*	BAR	78.4	0.001
Muscidae	*Muscina pascuorum*	JON	25.4	0.005
Muscidae	*Phaonia sp. iii*	BAR	28.6	0.003
Sarcophagidae	*Boettecheria cimbicis*	BAR	32.1	0.005
Scathophagidae	*Cordilura (Achaetella) sp.*	JON	87.5	0.001
Scathophagidae	*Neochirosa sp.*	FRN	26.2	0.018
Sciomyzidae	*Tetanocera plebeian*	BAR	68.2	0.001
Sciomyzidae	*Tetanocera sylvatica*	BAR	44.0	0.001
Sciomyzidae	*Tetanocera valida*	BAR	32.1	0.002
Sepsidae	*Sepsis punctum*	LAN	34.9	0.005
Sphaeroceridae	*Coproica ferruginata*	LAN	34.8	0.002
Sphaeroceridae	*Dahlimosina dahli*	JON	34.8	0.001
Sphaeroceridae	*Spelobia ochripes*	BAR	81.0	0.001
Tachinidae	*Eumea caesar*	MAR	25.0	0.012
Tachinidae	*Euthelyconychia vexans*	JON	76.0	0.001
Tachinidae	*Neomintho celeries*	CAR	34.0	0.001

Table 2.4: Correlation matrix of the environmental variables with the first two axes of the Canonical Correspondance Analysis.

	Land500	Land1000	Land1500	Veg1	Veg2
Axis 1	0.490	0.682	0.650	0.510	-0.626
Axis 2	0.499	0.443	0.323	0.664	0.402

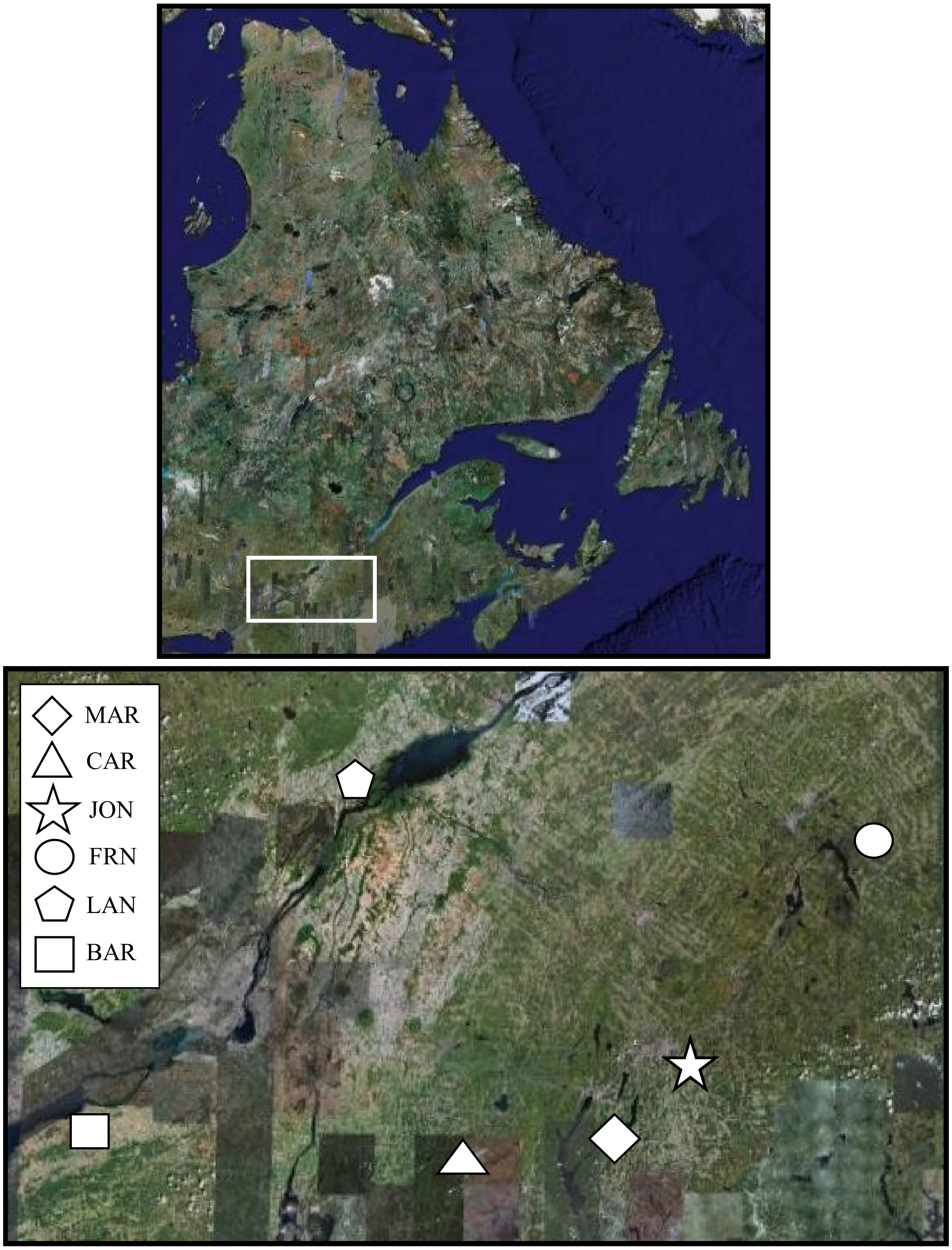

Figure 2.1: Location of study sites in southern Québec, Canada and northern Vermont, USA.

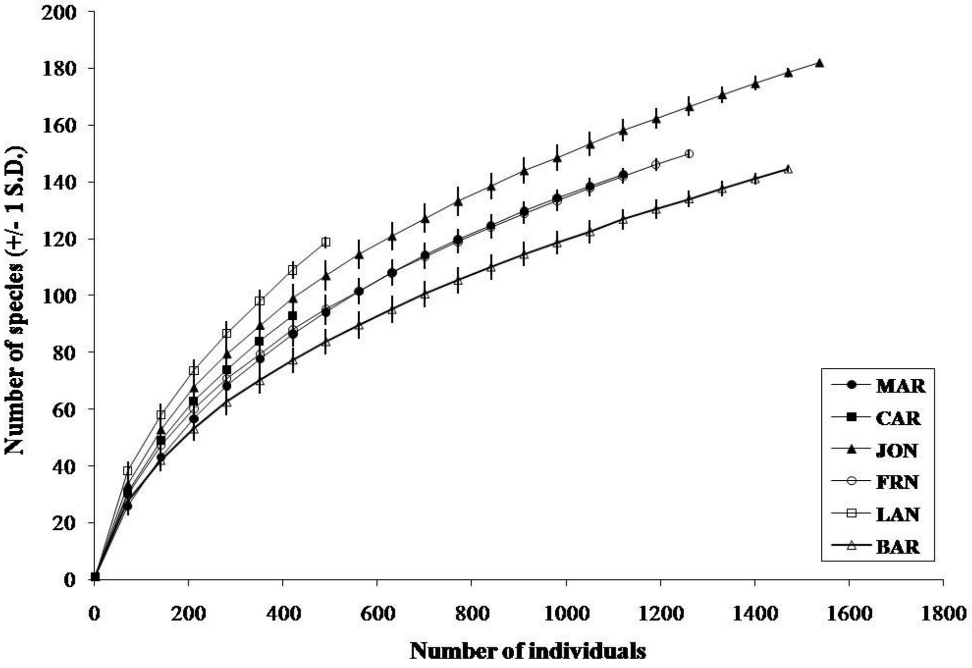

Figure 2.2: Rarefaction curves showing species richness (±SD) of Schizophora collected from six bog sites.

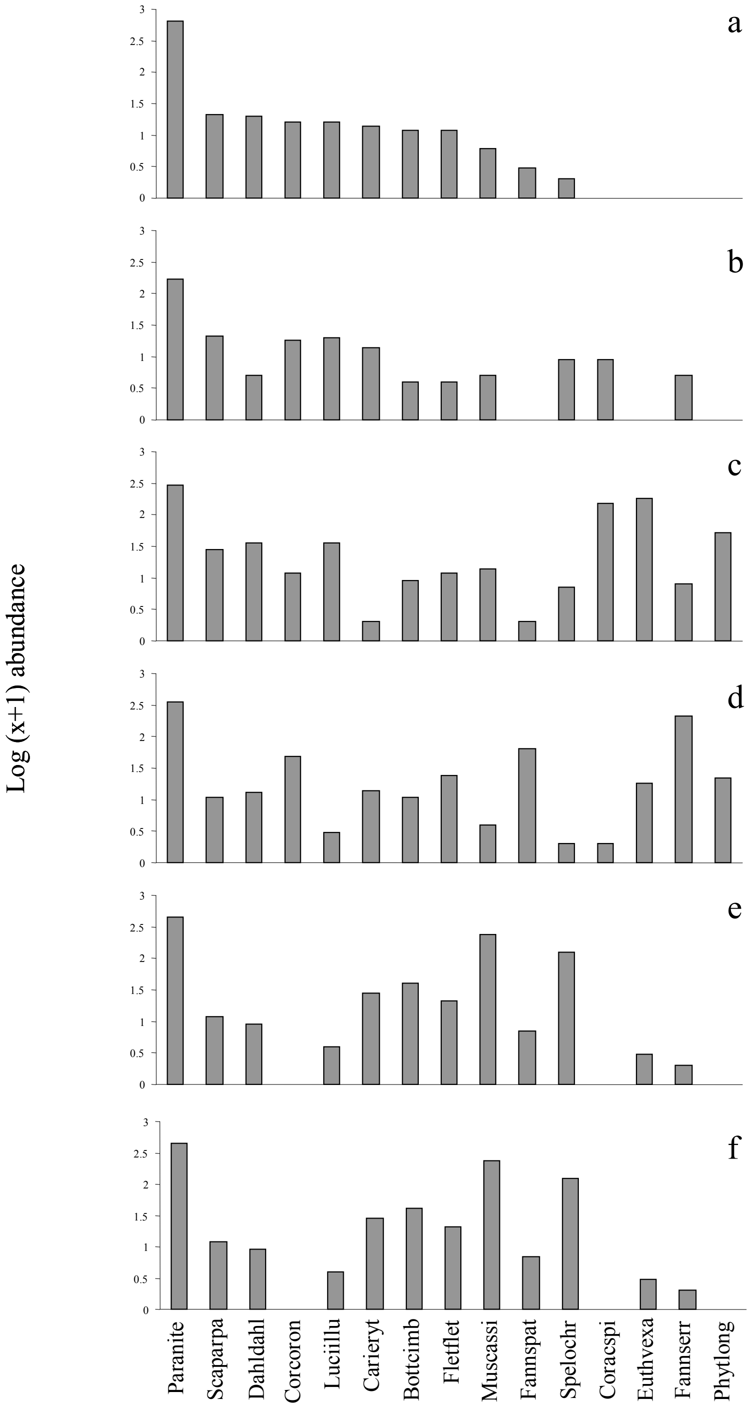

Figure 2.3: Rank abundance curves for the fifteen most abundant Schizophora species collected from a) MAR b) CAR c) JON d) FRN e) LAN and f) BAR. Species codes and names can be found in Appendix 2.1.

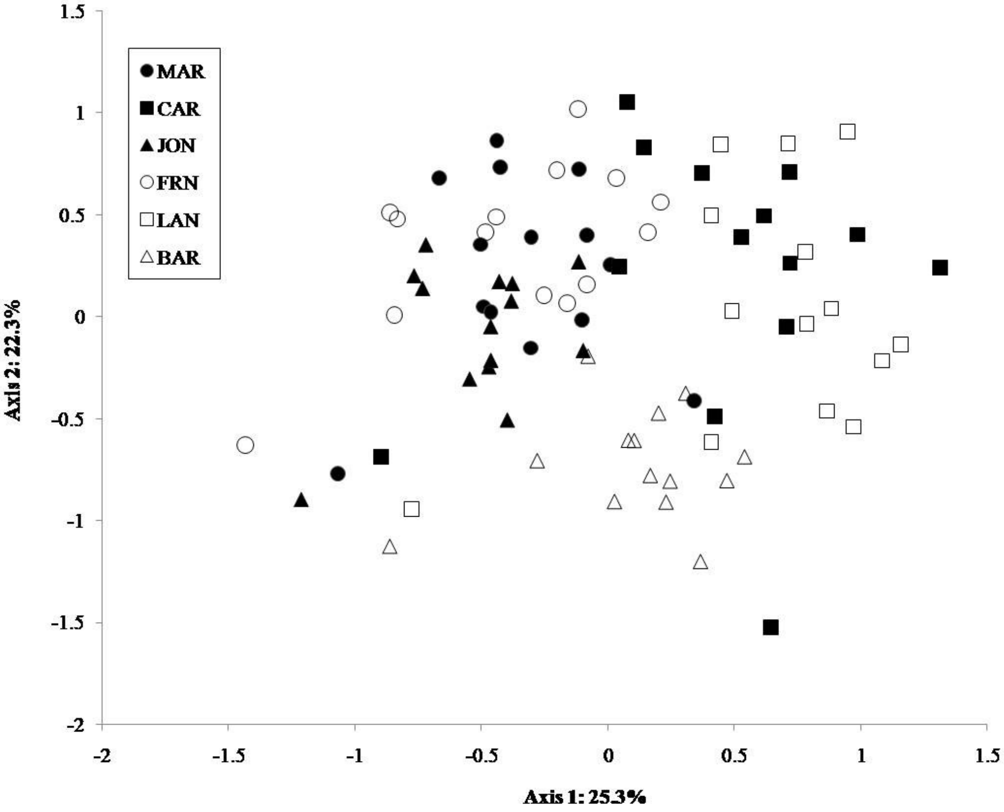

Figure 2.4: Two-dimensional solution for nonmetric multidimensional scaling showing Schizophora assemblages separated by bog site. Singletons and doubletons were omitted and data were log-transformed prior to analysis. Data points represent individual traps (individual pan traps, malaise traps and sweeping) pooled over sampling period. Ellipses designate general clustering of assemblages by site.

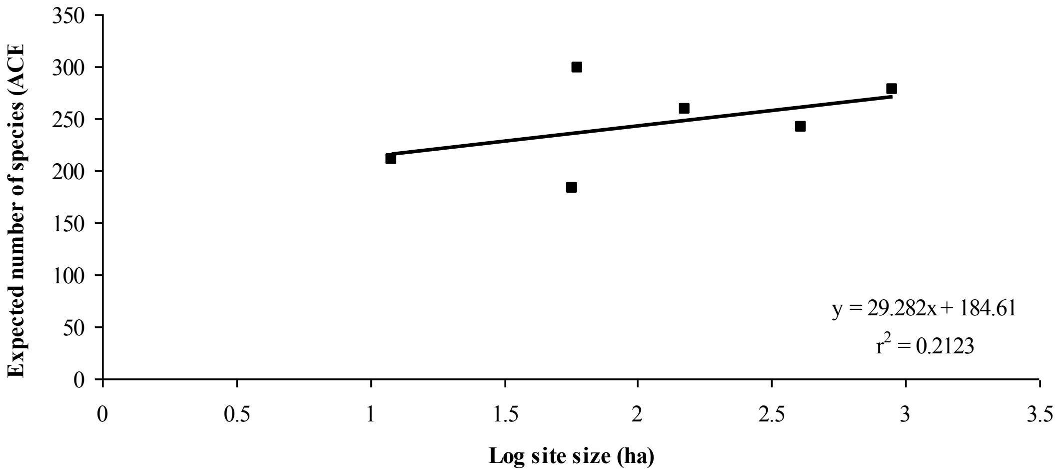

Figure 2.5: Linear regression of species richness vs. $\log_{10}$ site area ($p>0.05$).

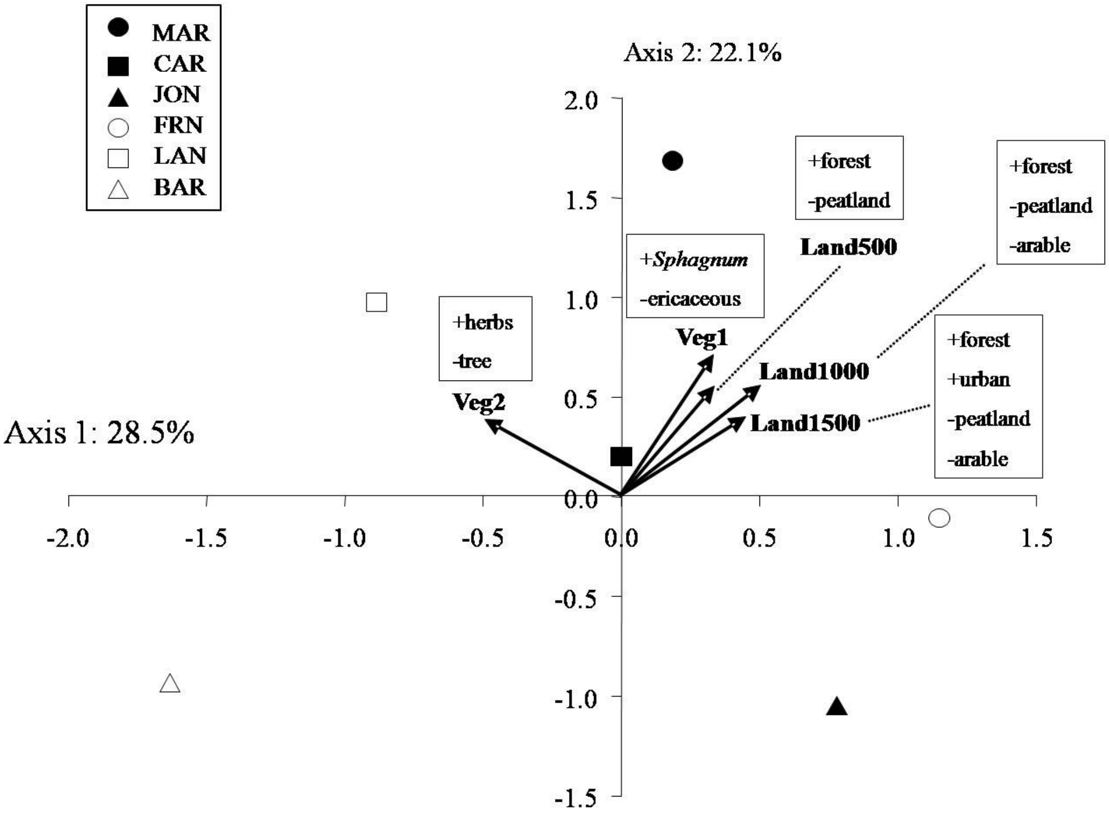

Figure 2.6: Canonical correspondence analysis of 5 environmental variables on Schizophora assemblages from the six sampled sites. Variables with the highest eigenvector coefficients are in boxes, adjacent to the relevant vector. + indicates a positive correlation and – indicates a negative correlation with the PCA-reduced environmental variable.

Appendix 2.1: Species and morphospecies of Schizophora collected from six study sites.

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
Acalyptratae								
Micropezidae	*Rainiera antennaepes* (Say)	Rainante	0	0	0	0	1	0
Tanypezidae	*Tanypeza luteipennis* Knab & Shannon	Tanylute	0	0	1	0	0	0
Psilidae	*Psila frontalis* Coquillett	Psilfron	1	0	0	0	0	0
Lonchaeidae	*Lonchaea* sp.1	Lonchspi	2	1	0	0	1	1
	Lonchaea sp.2	Loncspii	1	0	6	2	0	1
	Lonchaea sp.3	Lonspiii	0	0	0	0	0	1
	Lonchaea sp.4	Loncspiv	0	0	2	0	1	1
	Lonchaea sp.5	Lonchspv	0	0	3	0	0	0
	Protearomyia martinia McAlpine	Protmart	1	0	0	0	0	0
Ulidiidae	*Chaetops* sp.	Chaetosp	1	0	0	0	0	1
	Euxesta notata (Wiedemann)	Seiovibr	0	0	0	0	0	1
	Pseudotephritis vau (Say)	Euxenota	0	0	0	0	0	2
	Seioptera vibrans (Linnaeus)	Pseudvau	0	0	1	0	0	0
Platystomatidae	*Rivellia steyskali* Namba	Rivestey	0	0	0	0	0	4
Tephritidae	*Euaresta bella* (Loew)	Euarbell	0	1	0	0	0	28
	Myoleja limata (Coquillett)	Myollima	0	0	0	0	1	0
	Myoleja nigricornis (Doane)	Myolnigr	0	0	0	0	0	4
Piophilidae	*Actenoptera hilarella* (Zetterstedt)	Acterhila	0	0	1	0	0	0
	Parapiophila sp.	Parapisp	0	0	1	0	0	0
Clusiidae	*Clusia lateralis* (Walker)	Cluslate	0	1	0	1	1	0
	Sobarocephala atricornis Sabrosky	Sobalati	1	0	0	0	0	0
	Sobarocephala latifacies Sabrosky & Steyskal	Sobaatri	0	2	0	0	0	0
	Sobarocephala latifrons (Loew)	Sobalatr	1	0	0	0	0	0
Agromyzidae	*Agromyza* sp.1	Agromspi	3	0	0	3	0	0
	Agromyza sp.2	Agrmspii	0	0	0	0	1	0
	Ceratodontha sp.	Ceratosp	2	0	0	0	0	0
	Cerodontha (Cerodontha) dorsalis (Loew)	Cercerdo	0	0	0	0	1	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Cerodontha (Dizygomyza) magnicornis (Loew)	Cerdizma	10	0	0	4	5	0
	Cerodontha (Dizygomyza) morosa (Meigen)	Cerdizmo	0	0	0	3	1	0
	Cerodontha (Icteromyza) capitata (Zetterstedt)	Ceritcca	0	0	0	0	0	1
	Cerodontha (Icteromyza) churchillensis Spencer	Cerictch	0	0	1	0	0	0
	Cerodontha (Icteromyza) longipennis (Loew)	Cerictlo	9	0	1	2	1	0
	Cerodontha (Poemyza) inconspicua (Malloch)	Cerpoein	2	1	1	3	0	1
	Cerodontha (Poemyza) muscina (Meigen)	Cerpoemu	9	2	0	4	0	0
	Chromatomya sp.	Chromasp	2	0	0	7	0	0
	Liriomyza sp.	Liriomsp	3	0	0	0	2	0
	Ophiomyia sp.	Ophiomsp	0	0	0	0	1	0
	Paraphytomyza orbitalis (Melander)	Paraorbi	0	0	0	1	0	0
Opomyzidae	*Geomyza tripunctata* Fallén	Geomtrip	0	0	1	0	0	0
Periscelididae	*Cyamops halteratus* Sabrosky	Cyamhalt	2	0	0	0	3	0
	Cyamops nebulosus Melander	Cyamnebu	11	0	0	0	2	0
Milichiidae	*Desmometopa sordida* (Fallén)	Desmsord	0	0	1	0	0	0
	Leptometopa latipes (Meigen)	Leptlati	0	0	3	0	1	1
	Milichiella arcuata (Loew)	Miliarcu	0	0	3	0	1	0
	Milichiella lacteipennis (Loew)	Mililact	0	0	0	0	9	1
	Neophyllomyza quadricornis Melander	Neopquad	9	0	1	14	9	1
	Paramyia nitens (Loew)	Paranite	657	167	296	354	23	445
	Phyllomyza securicornis Fallén	Phylsecu	0	1	1	0	1	1
Dryomyzidae	*Dryomyza* sp.	Dryomysp	0	0	0	1	0	0
Sciomyzidae	*Antichaeta melanosoma* Melander	Antimela	0	1	0	0	1	0
	Dictya sp.	Dictyasp	1	0	0	0	0	2
	Limnia sp.	Limniasp	0	0	0	0	0	1
	Pteromicra apicata Loew	Pterapic	0	0	0	0	0	1
	Renocera amanda Cresson	Renolong	0	0	1	0	0	0
	Renocera longipes (Loew)	Renoaman	3	0	0	2	0	0
	Sepedon armipes Loew	Sepearmi	2	0	0	0	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Tetanocera ferruginea Fallén	Tetaferr	3	0	0	2	0	0
	Tetanocera plebeia Loew	Tetapleb	1	4	0	4	1	39
	Tetanocera silvatica Meigen	Tetasylv	3	0	1	2	0	20
	Tetanocera valida Loew	Tetavali	1	0	0	0	0	9
	Trypetoptera canadensis (Macquart)	Trypcana	4	0	0	1	0	0
Sepsidae	*Encita annulipes* (Meigen)	Enciannu	0	0	4	0	0	0
	Saltella sphondylii (Schrank)	Saltspho	20	1	14	5	0	0
	Sepsis flavimana Meigen	Sepsflav	0	0	0	1	0	0
	Sepsis punctum (Fabricius)	Sepspunc	4	5	3	11	36	0
Lauxaniidae	*Homoneura (Homoneura) cilifera* (Malloch)	Homhomci	0	0	2	0	1	1
	Homoneura (Homoneura) fraterna (Loew)	Homhomfr	0	0	0	0	0	1
	Homoneura (Tarsohomoneura) sheldoni (Coquillett)	Homtarsh	8	0	45	7	0	9
	Lauxania shewelli Pérusse & Wheeler	Lauxshew	0	0	0	0	0	5
	Minettia cana Melander	Minecana	0	0	4	1	0	0
	Minettia lupulina Fabricius	Minelupu	1	0	11	0	0	27
	Minettia lyraformis Shewell	Minelyra	1	0	0	0	1	0
	Trisapromyza vittigera (Coquillett)	Trisvitt	0	0	0	1	0	2
Chamaemyiidae	*Chamaemyia* sp.	Chamaesp	1	0	0	0	0	0
	Leucopis (Leucopis) sp.	Leuleusp	0	0	1	0	0	0
Heleomyzidae	*Suillia quinquepunctata* (Say)	Suilquin	0	0	0	0	0	2
Sphaeroceridae	*Apteromyia claviventris* (Strobl)	Apteclav	2	0	0	0	0	1
	Coproica acutangula (Zetterstedt)	Copracut	1	0	0	0	2	1
	Coproica ferruginata (Stenhammar)	Coprferr	0	1	0	3	16	3
	Coproica hirticula Collin	Coprcula	0	0	0	0	3	1
	*Coproica hirtula (*Rondani)	Coprhirt	2	0	1	1	4	2
	Coproica sp.	Coproisp	1	1	0	0	11	0
	Dahlimosina dahli (Duda)	Dahldahl	19	4	35	12	1	8
	Lotophila atra (Meigen)	Latoatra	0	1	0	0	0	1
	Minilimosia intercepta Marshall	Miniinte	0	1	0	1	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Minilimosia parva (Malloch)	Miniparv	1	0	1	1	1	3
	Minilimosia trogeri Roháček	Minitrog	0	0	0	0	1	0
	Opalimosina mirabilis (Collin)	Opalmira	1	0	0	0	0	0
	Pullimosina pullula (Zetterstedt)	Pullpull	0	0	0	1	0	1
	Spelobia algida Marshall	Spelalgi	0	0	0	0	0	1
	Spelobia bifrons (Stenhammar)	Spelbifr	0	1	0	1	0	1
	Spelobia clunipes (Meigen)	Spelclun	0	1	0	0	0	4
	Spelobia frustrilabis Marshall	Spelfrus	2	0	0	0	0	2
	Spelobia maculipennis (Spuler)	Spelmacu	1	0	0	0	0	0
	Spelobia ochripes (Meigen)	Spelochr	1	8	6	1	2	123
	Spelobia pappi Roháček	Spelpapp	1	0	0	0	0	0
	Spelobia quinata Marshall	Spelquin	0	1	4	0	0	0
	Telomerina sp.	Telomspi	0	0	0	0	0	1
Drosophilidae	*Amiota* sp.	Amiotasp	0	0	0	1	0	0
	Drosophila sp.1	Drosospi	3	3	12	0	2	5
	Drosophila sp.2	Drosspii	2	1	15	3	1	0
	Drosophila sp.3	Drospiii	3	1	0	0	13	1
	Drosophila sp.4	Drosspiv	6	2	2	2	0	19
	Drosophila sp.5	Drosospv	2	0	1	0	0	1
	Drosophila sp.6	Drosspvi	0	0	0	1	0	0
	Scaptomyza (Parascaptomyza) pallida (Zetterstedt)	Scaparpa	20	20	27	10	35	11
	Scaptomyza (Scaptomyza) sp.	Scascasp	2	0	2	0	2	0
Diastatidae	*Diastata* sp.1	Diastspi	0	1	3	1	1	0
	Diastata sp.2	Diasspii	0	0	2	0	0	0
	Diastata sp.3	Diaspiii	0	0	0	0	0	1
	Diastata sp.4	Diasspiv	0	0	3	0	0	0
Ephydridae	*Allotrichoma* sp.	Allotrsp	0	0	0	0	1	27
	Coenia sp.	Coeniasp	0	1	0	0	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Ditrichophora sp.	Ditricsp	0	0	0	0	0	1
	Hyadina subnitida Sturtevant & Wheeler	Hyadsubn	0	0	0	0	0	1
	Hydrellia griseola (Fallén)	Hydrgris	0	0	0	0	2	0
	Hydrellia nobilis (Loew)	Hydrnobi	0	1	0	0	0	0
	Hydrellia sp.	Hydrelsp	0	0	1	0	0	0
	Limnellia stenhammari (Zetterstedt)	Limnsten	0	0	1	0	0	0
	Notiphila (Dichaeta) caudata Fallén	Notdicca	1	0	0	0	11	0
	Notiphila (Dichaeta) sp.1	Notdispi	0	0	1	0	0	0
	Notiphila (Dichaeta) sp.2	Nodispii	0	0	0	0	0	1
	Ochthera borealis Clausen	Ochtbore	0	0	1	0	1	0
	Philygria debilis (Loew)	Phildebi	2	0	2	1	2	1
	Scatella (Scatella) favillacea Loew	Scascafa	0	2	4	1	0	3
	Scatella (Scatella) stagnalis (Fallén)	Scascast	1	6	1	3	2	25
	Scatophila sp.	Scatopsp	0	0	0	0	2	0
Chloropidae	*Apallates coxendix* (Fitch)	Apalcoxe	0	0	0	0	1	0
	Calamoncosis sp.	Calamosp	1	0	0	0	1	0
	Cetema elongatum (Meigen)	Ceteelon	0	0	3	0	0	0
	Chlorops sp.1	Chlorspi	6	7	5	1	1	0
	Chlorops sp.2	Chlospii	1	0	0	0	2	0
	Chlorops sp.3	Chlspiii	3	0	0	0	0	0
	Chlorops sp.4	Chlospiv	1	0	0	0	0	0
	Chlorops sp.5	Chlorspv	1	0	0	0	0	0
	Conioscinella flavescens (Tucker)	Coniflav	0	1	1	0	0	0
	Conioscinella sp.1	Coniospi	0	0	0	1	0	1
	Conioscinella sp.2	Conispii	0	0	0	0	1	0
	Elachiptera pechumani Sabrosky	Elacpech	2	0	0	0	1	0
	Elachiptera sp.1	Elachspi	1	0	0	0	0	1
	Elachiptera sp.2	Elacspii	0	0	1	0	0	0
	Epichlorops scaber (Coquillett)	Epicscab	1	1	3	1	0	9

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Gaurax dorsalis (Loew)	Gaurdors	0	0	1	0	0	0
	Gaurax pallidipes Malloch	Gaurpall	2	0	0	0	0	0
	Gaurax sp.1	Gauraspi	1	0	0	0	0	0
	Gaurax sp.2	Gaurspii	0	0	0	1	0	0
	Hippelates plebejus Loew	Hipppleb	0	0	0	0	1	6
	Incertella bispina (Malloch)	Incebisp	1	1	0	0	0	0
	Liohippelates bishoppi (Sabrosky)	Liohbish	0	0	0	0	6	15
	Malloewia diabolus (Becker)	Malldiab	3	0	0	0	0	0
	Malloewia nigripalpis (Malloch)	Mallnigr	4	0	2	0	1	5
	Meromyza sp.	Meromysp	3	0	1	0	0	1
	Olcella sp.	Olcellsp	0	0	0	0	5	0
	Olcella trigramma (Loew)	Olcetrig	0	0	0	0	1	1
	Oscinella sp.1	Oscinspi	0	1	0	0	1	0
	Oscinella sp.2	Oscispii	1	0	0	0	0	0
	Psilacrum arpidia (Malloch)	Psilarpi	0	0	0	1	0	0
	Rhopalopterum atriceps (Loew)	Rhopatri	2	5	0	0	1	0
	Rhopalopterum carbonarium (Loew)	Rhopcarb	0	1	1	0	2	1
	Rhopalopterum painteri (Sabrosky)	Rhoppain	0	0	1	0	1	0
	Rhopalopterum soror (Macquart)	Rhopsoro	0	0	1	0	0	0
	Rhopalopterum umbrosum (Loew)	Rhopumbr	0	0	0	0	0	1
	Thaumatomyia glabra (Meigen)	Thauglab	0	0	1	0	0	1
	Thaumatomyia grata (Loew)	Thaugrat	2	0	0	0	0	1
	Thaumatomyia pulla (Adams)	Thaupull	14	2	26	16	7	0
	Tricimba melancholica group	Tricmela	13	8	7	19	4	10
	Tricimba trisulcata (Adams)	Trictris	0	3	4	0	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
Calyptratae								
Scathophagidae	*Cordilura (Achaetella)* sp.	Cordacsp	0	8	148	1	0	0
	Cordilura (Cordilura) carbonaria Walker	Corcorca	1	1	7	0	0	0
	Cordilura (Cordilura) gagatina Loew	Corcorga	0	0	1	0	0	0
	Cordilura (Cordilura) ontario Curran	Corcoron	15	17	11	47	0	0
	Cordilura (Cordilura) variabilis Loew	Corcorva	0	0	0	1	0	0
	Cordilura (Cordilura) vierecki Cresson	Corcorvi	0	0	0	2	0	0
	Cordilura (Cordilurina) dimidiata (Cresson)	Corcrfdi	0	0	1	1	0	0
	Cordilura (Cordilurina) gracilipes Loew	Corcrdfl	5	7	1	22	1	0
	Cordilura (Cordilurina) pleuritica Loew	Corcrdgr	5	2	4	7	1	0
	Cordilura (Cordilurina) sp.	Corcrdpl	0	0	1	0	0	0
	Neochirosa sp.	Neochisp	0	0	0	11	1	0
	Orthacheta sp.	Orthacsp	2	1	4	1	0	0
	Parallelomma vittatum (Meigen)	Paravitt	0	0	0	0	2	0
	Scathophaga sp.	Scathosp	3	0	0	0	0	0
	Scathophaga stercoraria Linnaeus	Scathster	0	0	6	0	0	0
	Scathophaga futilis Malloch	Scatfuti	0	0	0	0	0	1
Fanniidae	*Fannia americana* Malloch	Fannamer	0	0	0	0	0	1
	Fannia atra (Stein)	Fannatra	4	0	0	26	0	0
	Fannia brooksi Chillcott	Fannbroo	0	0	2	1	1	0
	Fannia canicularis (Linnaeus)	Fanncani	0	0	2	11	0	3
	Fannia coracina (Loew)	Fanncora	0	1	0	1	0	0
	Fannia depressa (Stein)	Fanndepr	0	0	0	13	0	0
	Fannia difficilis (Stein)	Fanndiff	0	0	0	3	0	2
	Fannia fuscula (Fallén)	Fannfusc	0	2	0	0	0	0
	Fannia immaculata Malloch	Fannimma	0	0	0	4	0	0
	Fannia latifrons Malloch	Fannlati	1	0	1	3	0	0
	Fannia melanura Chillcott	Fannmela	1	0	2	0	0	0
	Fannia morrisoni Malloch	Fannmorr	0	0	0	1	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Fannia n. sp.	Fanninsp	1	0	0	0	0	0
	Fannia neopolychaeta Chillcott	Fannneop	0	0	3	1	1	10
	Fannia pallidiventris Malloch	Fannpall	0	0	1	0	0	0
	Fannia presignis Chillcott	Fannpres	0	0	0	2	0	0
	Fannia serrata Chillcott	Fannserr	0	4	7	207	0	1
	Fannia spathiophora Malloch	Fannspat	2	0	1	62	0	6
	Piezura graminicola (Zetterstedt)	Piezgram	1	0	1	0	1	0
Muscidae	*Azelia* sp.	Azelispi	3	0	0	0	0	0
	Caricea erythrocera Robineau-Desvoidy	Carieryt	13	1	13	13	46	27
	Caricea tinctinervis Malloch	Caritinc	0	0	0	0	0	2
	Coenosia (Coenosia) tigrina Fabricius	Coecoeti	0	2	0	1	0	0
	Coenosia (Opologaster) octopunctata (Zetterstedt)	Coehopoc	0	0	1	0	0	0
	Coenosia (Limosia) sp.1	Coelispi	2	1	5	1	22	13
	Coenosia (Limosia) sp.2	Colispii	0	0	9	3	0	0
	Coenosia (Limosia) sp.3	Colspiii	1	1	1	0	5	1
	Coenosia (Limosia) sp.4	Colispiv	0	0	0	0	1	1
	Coenosia (Limosia) sp.5	Coelispv	0	0	0	0	0	1
	Coenosia (Limosia) sp.6	Colispvi	0	0	0	0	0	3
	Coenosia (Limosia) triseta Stein	Coentris	0	0	11	0	1	11
	Eudasyphora cyanicolor Loew	Eudacyan	0	0	28	2	2	2
	Graphomya americana Robineau-Desvoidy	Grapamer	4	1	1	0	5	1
	Graphomya minuta Arntfield	Grapminu	0	0	0	0	1	0
	Graphomya transitionis Arntfield	Graptran	0	0	0	0	1	0
	Graphomya ungava Arntfield	Grapunga	1	1	0	0	0	0
	Hebecnema pallipes Malloch	Hebepall	1	1	0	0	1	0
	Helina sp.1	Helinspi	1	0	0	0	0	1
	Helina sp.2	Helispii	0	0	1	0	0	1
	Helina sp.3	Helspiii	0	0	1	0	0	1
	Helina sp.4	Helispiv	0	0	2	0	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Helina sp.5	Helinspv	0	0	1	1	0	0
	Helina sp.6	Helispvi	0	0	0	0	0	2
	Helina sp.7	Helspvii	0	0	2	0	0	1
	Helina sp.8	Hespviii	0	0	0	1	0	0
	Helina sp.9	Helispix	0	0	0	1	0	0
	Helina sp.10	Helinspx	0	0	1	0	0	0
	Helina sp.11	Helispxi	0	0	0	0	0	1
	Helina sp.12	Helspxii	0	0	0	0	0	1
	Hydrotaea armipes (Fallén)	Hydrarmi	0	0	5	0	0	1
	Hydrotaea militaris (Meigen)	Hydrmili	0	0	5	4	0	0
	Hydrotaea pilipes Stein	Hydrpall	0	0	1	0	0	0
	Hydrotaea ponti Vockeroth	Hydrpont	0	0	11	35	2	1
	Hydrotaea scambus (Zetterstedt)	Hydrscam	0	0	0	2	0	0
	Hydrotaea unispinosa Stein	Hydrunis	0	0	10	1	0	0
	*Limnospila albifrons (*Zetterstedt)	Limnalbi	1	2	12	5	14	6
	Lispe albitarsis Stein	Lispalbi	1	0	2	1	16	3
	Macrorchis ausoba (Walker)	Macrauso	1	0	0	0	1	0
	Morellia micans (Macquart)	Moremica	0	0	3	5	1	0
	Morellia podagrica (Loew)	Morepoda	0	0	14	30	0	0
	Musca autumnalis DeGreer	Muscautu	4	0	47	3	1	4
	Musca domestica Linnaeus	Muscdome	3	1	26	5	0	1
	Muscina assimilis (Fallén)	Muscassi	5	4	13	3	18	234
	Muscina pabulorum Meigen	Muscpabu	0	0	0	0	0	1
	Muscina pascuorum (Meigen)	Muscpasc	9	1	12	2	1	2
	Mydaea brevipilosa Malloch	Mydabrev	0	0	2	0	0	0
	Mydaea discimana Malloch	Mydadisc	1	0	1	1	0	1
	Mydaea neglecta Malloch	Mydanegl	0	1	10	5	0	6
	Mydaea neobscura Snyder	Mydaneob	0	0	1	0	0	0
	Mydaea obscurella Malloch	Mydaobsc	1	0	4	1	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Mydaea occidentalis Malloch	Mydaocci	0	0	7	5	0	1
	Myospila meditabunda (Fabricius)	Myosmeti	9	2	11	14	1	1
	Neodexiopsis calopyga Loew	Neodcalo	0	0	0	0	0	8
	Pentacricia aldrichii Stein	Pentaldr	0	0	0	1	5	6
	Phaonia sp.1	Phaonspi	0	0	1	0	0	2
	Phaonia sp.2	Phaospii	1	0	1	3	2	0
	Phaonia sp.3	Phaspiii	0	0	0	0	0	4
	Phaonia sp.4	Phaospiv	1	0	3	3	0	0
	Phaonia sp.5	Phaonspv	0	0	0	1	0	0
	Phaonia sp.6	Phaospvi	0	0	0	0	0	1
	Phaonia sp.7	Phaspvii	0	0	1	0	0	0
	Phaonia sp.8	Phspviii	0	0	0	1	0	0
	Phaonia sp.9	Phaospix	0	0	0	1	0	0
	Polietes orichalceoides Huckett	Polioric	0	0	1	0	0	0
	Potamia querceti (Bouché*)*	Potaquer	1	0	0	0	0	0
	Pseudocoenosia sp.	Pdeudspi	0	1	0	0	0	0
	Schoenomyza chrysostoma Loew	Schochry	0	0	0	0	1	0
	Thricops diaphanus (Wiedemann)	Thridiap	0	0	1	0	0	0
	Thricops innocuus (Zetterstedt)	Thriinno	0	0	0	1	0	0
Calliphoridae	*Angioneura* sp.	Angionsp	2	0	0	0	0	0
	Calliphora livida Hall	Calllivi	0	1	1	0	0	0
	Calliphora stelviana (Brauer & Bergenstamm)	Callstel	0	1	1	4	0	0
	Lucilia coeruleiviridis Macquart	Lucicoer	0	1	1	0	0	1
	Lucilia illustris (Meigen)	Luciillu	15	19	35	2	12	3
	Lucilia sericata (Meigen)	Luciseri	0	5	0	0	0	0
	Lucilia silvarum (Meigen)	Lucisilv	1	1	1	0	1	0
	Phormia regina (Meigen)	Phorregi	0	0	5	0	5	1
	Pollenia angustigena Wainwright	Phorangu	2	1	0	0	0	0
	Pollenia pediculata Macquart	Pollpedi	26	5	13	0	0	24

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Pollenia rudis (Fallén)	Pollrudi	3	1	1	0	0	0
	Protocalliphora sp.	Protospi	0	0	1	0	0	0
Sarcophagidae	*Blaesoxipha atlanis (*Aldrich)	Blaeatla	0	0	0	0	0	1
	Blaesoxipha (Acridiophaga) kyrtonidion Pape	Blaacrky	0	0	2	2	0	0
	Blaesoxipha (Acridiophaga) reversa Aldrich	Blaacrre	4	0	4	2	1	0
	Blaesoxipha (Tephromyia) amblycoryphae (Coquillett)	Blatepam	0	0	0	0	0	1
	Blaesoxipha (Tephromyia) hunteri Hough	Blatephu	0	0	0	0	1	0
	Boettecheria bisetosa Parker	Bottbise	0	0	5	0	2	3
	Boettecheria cimbicis (Townsend)	Bottcimb	11	3	8	10	8	40
	Boettecheria latisterna Parker	Bottlati	2	1	3	1	0	3
	Brachicoma devia Fallén	Bracdevi	0	0	2	0	19	25
	Emblemasoma sp.	Emblemsp	0	0	0	0	0	1
	Fletcherimyia fletcheri (Aldrich)	Fletflet	11	3	11	23	3	20
	Helicobia rapax (Walker)	Helirapa	1	0	0	0	4	2
	Microcerella sp.	Microcsp	0	0	0	0	0	2
	Ravinia acerba Walker	Raviacer	5	0	2	13	0	0
	Ravinia anxia Walker	Ravianxi	0	0	2	6	0	6
	Ravinia pusiola (van der Wulp)	Ravipusi	0	0	1	0	0	0
	Ravinia querula Walker	Raviquer	4	1	1	4	0	4
	Ravinia stimulans Walker	Ravistim	12	4	4	1	4	23
	Sarcophaga aldrich Parker	Sarcaldr	0	0	0	0	0	2
	Sarcophaga bullata Parker	Sarcbull	0	0	0	0	1	0
	Sarcophaga nearctica (Parker)	Sarcnear	0	1	1	1	1	0
	Sarcophaga sarraceniae Riley	Sarcsarr	0	1	3	2	0	0
	Sarcophaga sinuata Meigen	Sarcsinu	3	2	0	1	7	6
	Sarcophaga subricina Rohdendorf	Sarcsubr	0	3	0	0	0	4
Tachinidae	*Acemya tibialis* Coquillett	Acemtibi	0	1	0	1	0	0
	Actia diffidens Curran	Actidiff	1	0	6	1	0	0
	Actia dimorpha O'Hara	Actidimo	2	0	0	0	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Actia interrupta Curran	Actiinter	1	0	0	0	0	1
	Admontia degeerioides (Coquillett)	Admodege	1	0	0	0	0	0
	Allophorocera delecta (Curran)	Allodele	0	0	2	0	0	0
	Archytas apicifer (Walker)	Archapic	2	0	0	0	0	0
	Archytas aterrimus (Robineau-Desvoidy)	Archater	0	3	6	2	1	13
	Arctophy sp.	Arctopsp	1	0	0	0	0	0
	Athrycia cinerea (Coquillett)	Athrcine	0	0	3	0	0	0
	Belvosia unifasciata (Robineau-Devoidy)	Belvunif	2	0	0	0	0	0
	Billaea sp.	Billaesp	0	0	0	0	1	0
	Blondelia eufitchiae (Townsend)	Bloneufi	0	0	3	0	1	0
	Carcelia reclinata (Aldrich & Webber)	Carcrecl	1	0	1	4	0	1
	Compsilura concinnata (Meigen)	Compconc	2	2	1	0	0	0
	Cylindromyia sp.	Cylindsp	0	0	0	0	0	1
	Cyrtophleba coquiletti (Aldrich)	Cyrtcoqu	0	2	1	1	0	0
	Epalpus signifer (Walker)	Epapsign	0	2	0	0	1	0
	Eribella exilis (Coquillett)	Eribexil	0	0	0	0	0	1
	Euexorista sp.	Euexorsp	0	0	1	10	0	0
	Eumea caesar (Aldrich)	Eumecaes	7	0	0	0	1	0
	Euthelyconychia vexans (Curran)	Euthvexa	0	0	180	17	21	2
	Exorista dydas (Walker)	Exordyda	0	0	2	0	1	0
	Gonia distincta Smith	Gonidist	0	0	5	1	0	0
	Graphogaster sp.	Graphosp	1	0	0	0	0	0
	Gymnocheta sp.	Gymnocsp	0	0	0	1	0	0
	Houghia sternalis (Coquillett)	Hougster	0	0	0	0	1	0
	Hubneria estigmemensis (Sellers)	Hubnesti	1	0	0	0	0	0
	Lespesia frenchii (Williston)	Lespfren	1	4	0	3	0	0
	Linnaemya nigriscens Curran	Linnnigr	0	0	0	3	0	0
	Linnaemya sp.	Linnaesp	4	0	0	1	0	0
	Linnaemya tessellata (Brooks)	Linntess	1	1	1	1	0	0

Family	**Species**	**Code**	**MAR**	**CAR**	**JON**	**FRN**	**LAN**	**BAR**
	Lixophaga sp.	Lixophsp	0	1	1	6	1	1
	Lixophaga unicolor (Smith)	Lixounic	2	0	8	13	4	0
	Lydella sp.	Lydellsp	1	0	1	0	0	0
	Muscopteryx evexa (Reinhard)	Muscevex	0	0	0	1	0	0
	Myiopharus dorsalis (Coquillett)	Myiodors	0	0	0	0	0	1
	Neomintho celeris (Townsend)	Neomcele	0	17	2	1	1	4
	Nilea sp.	Nileaspi	0	0	1	1	0	0
	Oswaldia sp.	Oswaldsp	0	0	0	1	0	4
	Panzeria arcuata (Tothill)	Panzarcu	0	0	2	0	0	0
	Panzeria nigropalpis (Tothill)	Panznigr	0	0	1	2	0	0
	Panzeria platycarina (Tothill)	Panzplat	0	0	1	1	0	0
	Panzeria sp.	Panzersp	0	1	0	0	0	0
	Pararchytas decisus (Walker)	Paradeci	2	0	0	0	0	0
	Patelloa pachypyga (Aldrich & Webber)	Patepach	0	6	7	3	0	0
	*Periscepsia clesides (*Walker)	Pericles	0	0	32	8	8	0
	Periscepsia laevigata van der Wulp	Perilaev	1	0	1	1	0	0
	Phebellia helvina (Coquillett)	Phebhelv	0	0	0	1	0	0
	Phryxe pecosensis (Townsend)	Phrypeco	0	0	0	4	0	0
	Phytomyptera longicornis (Coquillett)	Phytlong	0	0	50	21	0	0
	Phytomyptera tarsalis (Coquillett)	Phyttars	0	0	0	0	0	3
	Phytomyptera usitata (Coquillett)	Phytusit	0	7	1	0	0	0
	Phytomyptera vitinervis (Thompson)	Phytviti	1	0	0	1	6	2
	Platymya confusionis (Sellers)	Platconf	0	1	1	0	0	0
	Prooppia crassiseta (Aldrich & Webber)	Proocras	1	0	1	1	0	1
	Pseudochaeta argentifrons Coquillett	Pseuarge	0	0	0	0	0	1
	Siphona (Ceranthia) sp.	Sipcersp	0	0	0	2	2	0
	Siphona (Siphona) hokkaidensis Mesnil	Sipsipho	3	0	0	2	0	0
	Siphona (Siphona) intrudens Curran	Sipsipin	0	0	6	0	1	0
	Siphosturmia phyciodis (Coquillett)	Siphphyc	0	0	1	0	0	0

Family	Species	Code	MAR	CAR	JON	FRN	LAN	BAR
	Spallanzania hesperidarum (Williston)	Spalhesp	0	0	0	1	0	0
	Spathidexia dunningii (Coquillett)	Spatdunn	0	0	6	1	0	0
	Spathidexia reinhardi (Arnaud)	Spatrein	0	0	9	0	0	0
	Strongygaster triangulifer (Loew)	Strotria	0	0	1	0	0	0
	*Tachinomyia nigricans (*Webber)	Tachnigr	0	0	2	0	0	0
	Thelaira americana Brooks	Thelamer	0	0	0	0	1	0
	Uramya pristis (Walker)	Urampris	0	0	0	2	1	1
	Vibrissina leibyi (Townsend)	Vibrleib	0	0	0	1	0	0
	Voria ruralis (Fallén)	Vorirura	0	0	1	1	0	0
	Wagneria sp.	Wagnesp	0	0	1	0	0	0
	Winthemia vesiculata (Townsend)	Wintvesi	1	0	1	0	0	0
	Zelia vertebrata (Say)	Zelivert	0	0	0	0	2	0

Appendix 2.2: Averaged percent cover of nine vegetation classes at six study sites.

	Ericaceous shrubs	*Sphagnum* spp.	Other mosses	Grasses	Ferns	Herbaceous plants	Trees	Litter	Lichens
MAR	55.4	93.8	-	57.1	-	7.6	17.9	2.7	2.6
CAR	56.7	96.3	-	21.2	1.0	1.0	23.8	4.3	11.8
JON	82.5	69.2	14.8	7.9	-	0.8	18.8	50.4	9.0
FRN	28.3	97.9	-	66.7	-	11.7	26.7	2.1	2.9
LAN	58.3	95.4	5.2	12.8	16.7	37.9	8.9	10.0	2.1
BAR	67.5	47.9	65	31	-	0.08	6.4	30.4	0.96

Appendix 2.3: Percent cover of land use category around six study sites at 500, 1000, 1500 and 2000 m.

Land use category	Distance (m)	MAR	CAR	JON	FRN	LAN	BAR
Arable	500	5	-	15	-	-	45
	1000	15	-	30	-	20	55
	1500	30	20	45	-	20	70
	2000	45	45	60	-	30	60
Urban	500	-	-	-	-	-	-
	1000	-	-	-	-	-	-
	1500	5	5	5	-	-	-
	2000	5	5	10	-	-	-
Forest	500	91	30	55	25	30	-
	1000	83	40	50	50	30	10
	1500	58.5	40	35	80	30	5
	2000	43	25	20	78	30	-
Peatland	500	2	45	25	75	70	55
	1000	1	20	10	50	50	35
	1500	0.75	10	7.5	20	50	25
	2000	1	5	5	20	40	35
Water	500	2	25	5	-	-	-
	1000	1	40	10	-	-	-
	1500	0.75	25	7.5	-	-	-
	2000	1	20	5	2	-	-
Other	5000	-	-	-	-	-	-
	1000	-	-	-	-	-	-
	1500	5	-	-	-	-	-
	2000	5	-	-	-	-	-

CHAPTER 3: GENERAL CONCLUSION

The findings of this study have enhanced the knowledge of which environmental variables affect Schizophora assemblage diversity and composition in temperate-zone bogs of the eastern Nearctic. Bogs in the temperate-zone of North America are present as relict ecosystems of boreal diversity and should not be ignored in biodiversity studies. Over 300 species of flies were collected during this research which supports previous findings that bogs support diverse Diptera assemblages which represent an ideal group to use in ecological studies examining the impacts of habitat fragmentation and disturbances on biodiversity. Information on how vegetation and landscape conditions impact bog-inhabiting flies in North America is lacking and this study provides valuable baseline data on Diptera diversity in these important, yet threatened ecosystems.

The importance of including vegetation structure and land use factors in biodiversity studies in fragmented landscapes was highlighted by examining the influence of surrounding land use and vegetation composition of the sites on the composition of Schizophora assemblages. These factors accounted for a high percentage of variation in species composition at the bog sites and support other studies which have shown that vegetation structure and landscape conditions significantly affect arthropod species compositions. The species compositions of all sites except one were positively influenced by a high cover of forested land and low cover of arable land up to 1500 m from the sampling location. Other authors have found that complex habitat shape and intermediate levels of disturbance in the habitat studied lead to high organismal diversity. It is possible that these factors may explain the high Schizophora diversity found in Johnville Bog and the Réserve écologique des tourbières-de-Lanoraie.

The other objective of this study was to investigate how bog size affected the species richness, evenness and similarity of Schizophora assemblages. Bog size had no significant impact on species richness and contrary to my predictions, a positive species-area relationship was not found. The edges around the bogs were not impermeable to flies entering from the surrounding habitat matrix and this flow in and out of the bogs possibly explains the lack of pattern between bog size and species richness of Schizophora. Habitat specialists generally show stronger species-area relationships and bog-associated Diptera may follow this pattern, although this study was not designed to address this relationship for particular species. There was no pattern found for diversity and evenness of the Schizophora assemblages with bog size, contrary to my expectations. The smallest site, Marlington Bog, had the lowest diversity and evenness, which indicates that small bogs with a high forest cover in the landscape may act more like a forest than a bog, as a high forest cover may act as a barrier for certain flies that are unable to move through densely treed areas. The finding from the Bray-Curtis index support the results of the NMDS ordination that there was a great deal of species overlap between the sites, though some species compositions were more similar than others.

Contrary to what I had expected, the assemblages did not show a nested pattern, with different species being added to the overall species pool as bog size increased. Though a positive species-area relationship has been found for birds in peatlands, the results obtained examining the influence of bog size on the diversity of Schizophora species assemblages demonstrate that area is not an adequate predictor of diversity patterns for Diptera in eastern Nearctic bogs.

My study has shown that in addition to local habitat factors, larger landscape-level factors such as land use need to be considered in biodiversity conservation studies. My results indicate that intermediate-sized bogs with moderate amounts of arable land and undisturbed forest up to 1500 m around them support diverse Schizophora assemblages. Land-use management decisions should focus on preserving a forested buffer zone between bogs and agricultural activity and protecting remaining parcels of forested land to maintain diverse Schizophora assemblages.