NESTED PATTERNS OF BETA-DIVERSITY IN FOREST DIPTERA

Valérie Lévesque-Beaudin Department of Natural Resource Sciences McGill University, Montreal August, 2009

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TABLE OF CONTENTS

LIST OF TABLES	iv
LIST OF FIGURES	V
LIST OF APPENDICES	vi
ACKNOWLEDGEMENTS	vii
PREFACE	viii
PREFACE	viii ix
PREFACE	viii ix x

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

General introduction	1
Insects in forests	2
Species diversity across spatial scales	3
Additive partitioning of species richness	5
Diversity patterns in forest arthropods	7
Diptera diversity	10
Studies on forest Diptera	11
Objectives:	14
Hypotheses and predictions	14
REFERENCES	15
CONNECTING STATEMENT	28

CHAPTER 2: NESTED PATTERNS OF BETA-DIVERSITY IN FOREST DIPTERA

ABSTRACT	29
INTRODUCTION	60
MATERIALS AND METHODS	3
Study sites and sampling design	3
Diptera sampling and preparation	\$4
Environmental variables	5
Statistical analyses	6
RESULTS	8
Species diversity	8
Diversity patterns across spatial scales	0
DISCUSSION4	1
REFERENCES4	8

4
4

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

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PREFACE

The thesis is composed of three chapters; one of which is an original manuscript that will be submitted for publication in a refereed journal.

Chapter 1

This chapter is a general introduction and literature review.

Chapter 2

This chapter is a manuscript in preparation for submission to a refereed journal: Lévesque-Beaudin, V. and T. A. Wheeler. Nested patterns of beta-diversity in forest Diptera.

Chapter 3

This chapter is a general conclusion.

CONTRIBUTION OF AUTHORS

V. Lévesque-Beaudin designed the research and was responsible for field sampling, specimen preparation, identification of Diptera specimens, analyzing the data and writing the manuscript. T. A. Wheeler supervised the research, edited the manuscript, provided facilities and financial support for the equipment, the field season, the specimen preparation and conference travel.

ABSTRACT

Nested patterns of diversity in temperate forest Diptera (Schizophora) were assessed, to determine the scale contributing the most to fly diversity in this habitat. Fieldwork was carried out in June-July 2008 in three southwestern Quebec forest fragments, using three spatial scales (tree, stand, and site). Diptera species diversity (239 species) and composition was non-random at all scales selected. These scales did not contribute equally across the different groups, as shown by different diversity patterns. Smaller scales seem to structure Diptera species composition (β_1 : between trees), as well as the two major taxonomic subgroups (Calyptratae and Acalyptratae). Common species were also more important at finer scales (α_1 : within trees), while rare species varied more at broader scales (β_3 : between sites). The scale contributing the most to γ -diversity was variable across the different groups, although β_1 was generally strongest. Environmental variables supported species composition only weakly.

RÉSUMÉ

Les patrons de diversité emboitée sur les diptères (Schizophora) de forêt tempérée ont été obtenus en déterminant l'échelle contribuant le plus à la diversité. Le terrain a été effectué (juin-juillet 2008) dans trois fragments forestiers du sudouest du Québec, utilisant trois échelles spatiales (arbre, parcelle, site). La diversité des diptères (239 espèces) et la composition en espèces n'était pas aléatoire à toutes les échelles. Ces échelles n'étaient pas également importantes pour les différents groups. Les plus petites échelles semblent structurer davantage la composition en espèces des diptères, ainsi que des deux groupes taxonomiques : Calyptratae et Acalyptratae. Les espèces communes étaient aussi principalement influencées par les petites échelles, alors que les espèces rares étaient davantage importantes à de plus larges échelles. L'échelle contribuant le plus à la diversité du pool était β_1 (entre les arbres). Les variables environnementales supportaient faiblement la composition en espèces.

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

"Numerus specierum in entomologia fere infinitus et nisi in ordinen redigantur, chaos semper erit entomologia." [The number of species in entomology is almost infinite, and if they are not brought in order entomology will always be in chaos.]

- J. C. Fabricius (1778) Philosophia entomologica

General introduction

Forests cover 30.3% of the global land area (Food and Agriculture Organization of the United Nations 2009). In Canada, 402.1 million hectares are covered by forests and other wooded lands, representing 10% of the world's forest cover (Natural Resources Canada 2008). One of the most biologically diverse forest types in Canada is the temperate deciduous forest, which is limited to five regions in the world (eastern North America, western and central Europe, eastern Asia, eastern Europe and Patagonia) (Röhrig 1991).

In Canada, temperate deciduous forest is situated in the Hemlock-White Pine-Northern Hardwoods regions, specifically in the Great Lakes-St. Lawrence division, where the climate is rigorous, with short growing seasons and cold and snowy winters (Barnes 1991). In this region the dominant forest type is beech – sugar maple (Smith 1980), characterized by the occurrence of *Acer saccharum* Marsh (Aceraceae), codominant with *Fagus grandifolia* Ehrh (Fagaceae) (Barnes 1991).

In southern Quebec, this forest type is generally found on well-drained upper slopes below 490 m elevation, and associated with white ash (*Fraxinus americana*: Oleaceae), white pine (*Pinus strobus*: Pinaceae), hemlock (*Tsuga spp.*: Pinaceae), and aspens (*Populus spp.*: Salicaceae) (Smith 1980).

Because biodiversity is high in temperate deciduous forests (Franklin 1988), the ecosystem is of global significance for conservation (Norton 1996), as well as providing opportunities for studies of biodiversity across a range of taxa and ecological groups.

Insects in forests

Arthropods are a major component of the biodiversity in temperate deciduous forests, often representing over 57% of the recorded species (Schowalter 2006). Their relative diversity is mainly explained by their small size, coupled with their dispersal ability, allowing them to occupy smaller niches (May 1978). Other factors are also important: their short generation time, which increases the potential rate of adaptation; their broad range of trophic groups, which limits inter-specific competition; the high number of generalist species; and their behavior (Grimaldi and Engel 2005, Schowalter 2006). Although insects are present almost everywhere, they are often unnoticed in forests, because of their size, unless massive outbreaks occur (Dajoz 2000). They can be found among five major forest biotopes: canopy, tree trunk, ground and low vegetation, leaf litter, and soil (Stork 1988). The distribution of species within these biotopes varies with their requirements; for example, some are restricted to tree trunks, while others will favor different canopy levels, or even just the sunny or shady parts of the tree (Stork 1988).

The ecological roles occupied by insects are numerous and diverse. They occupy several guilds including plant eaters, decomposers, pollinators, predators and parasites (Dajoz 2000). Each guild is further divided into more specialized groups. The phytophagous insects, for example, include leaf eaters, meristem eaters, root eaters, sap suckers, gall makers, fruit and seed eaters, and xylophagous members (Dajoz 2000).

Despite their ecological importance and dominance in forests, most insects are poorly studied and little is known about their biology, distribution, diversity, vulnerability and conservation (Norton 1996, New 1999, Hughes *et al.* 2000, Miller *et al.* 2008). Although about one million described species are known (Hammond 1992, Grimaldi and Engel 2005), it is estimated that at least five million are still unnamed (Hammond 1992). The vast majority of the described species are distributed among four orders: Coleoptera (38% of all insect species), Lepidoptera (16%), Hymenoptera (13%) and Diptera (12%) (Kitchings and Walton 1991, Grimaldi and Engel 2005).

Species diversity across spatial scales

Arthropod communities are usually made up of a few abundant species and of a large number of rare species (Tokeshi 1999, Dajoz 2000). Rare species, represented by only one or two specimens can comprise more than 30% of all specimens collected in samples (DeVries et al. 1999, Novotny and Basset 2000, Gering et al. 2003, Beaulieu and Wheeler 2005, Caterino 2007, Nielsen and Nielsen 2007, Ewers and Didham 2008). The relative number of rare and common species can be visualized through species abundance distributions (SAD) (Hirao et al. 2006), which allow comparison of proportions of rare and common species across scales (e.g., Larrivée 2009) and the contribution of each group to patterns at each scale (Tokeshi 1999). Sampling at larger spatial scales increases the chances to encounter rare species (Gering et al. 2003, Deblauwe et al. 2008, Hui 2008); this is typically illustrated by the long tail of a left-skewed lognormal distribution (Tokeshi 1993, 1999, Hubbell 2001, Magurran 2004, McGill et al. 2007), showing the patchy or restricted distribution of rare species, compared to the usual wider spatial range of common species (Tokeshi 1999). Species abundance distributions have the power to shed light on understanding communities in general (McGill et al. 2007), as well as on the processes behind the species diversity in an assemblage (Magurran 2004). They also allow species richness patterns to be clearly displayed (Magurran 2004).

The identification of diversity patterns across spatial scales has always been a central theme in community ecology (Wiens 1989, Levin 1992, Tokeshi 1993,

1999, Leibold *et al.* 2004, Schowalter 2006). It has been shown that when patterns at local and regional scales are considered together, a more complete picture of overall patterns and dynamics expressed by species in an ecosystem may emerge (Ricklefs and Schluter 1993). Biodiversity studies usually search for non-random patterns in species diversity, and then explore further to identify the processes underlying those patterns (Levin 1992, Tokeshi 1999, Gering *et al.* 2003, Summerville *et al.* 2003a, MacNally *et al.* 2004, Larrivée 2009), spatial scaling is useful for that purpose. Even though consideration of scaling approaches would appear to be fundamental in ecology, it has been neglected in several studies (Schowalter 2006). Wiens *et al.* (1986) presented the importance of using a scaling approach in ecology and defined three general scales (i.e., regional scale, biogeographic scale, scale of the closed system) that can be used. It has also been pointed out that the approach has to be correctly used with the appropriate scale (Nilsson *et al.* 2001) in order to identify the actual dynamics and patterns of the system under study, and not just artefacts arising from the scale (Wiens 1989).

There is no standard in ecology to define the spatial scale of a local community (Loreau 2000); they are usually user-defined. A number of factors that vary from species to species have to be considered in the choice of scale for studying population dynamics, social structure, individual dispersal range, and the ecological processes that are the focus of the study (Wiens *et al.* 1986, Levin 1992). The last, understanding how the scaling approach affects ecological processes, is, in fact, a major frontier in ecology (Thompson *et al.* 2001). These processes probably control species diversity, at least in part (Gonzalez-Megias *et al.* 2007), and are dominant and perceptible at different scales, if not scale specific (Levin 1992, Godfray and Lawton 2001, Schowalter 2006). Communities can exhibit heterogeneity at a variety of scales (Levin 1992, McLaughlin and Roughgarden 1993, Tokeshi 1993), reflecting the complexity of their interacting species, but also their unique way of experiencing the environment (Levin 1992). This is because species within a community have different habitat requirements and dispersal capacity (Novotny and Weiblen 2005, Cadotte 2006, Hirao *et al.*

2008a). Hence, the environmental heterogeneity (Wiens 1989, Hirao *et al.* 2008a, Hirao *et al.* 2008b) and the patterns detected will depend on the scales selected (Levin 1992, Palmer and White 1994, Rosenzweig 1995, Leibold *et al.* 2004, MacNally *et al.* 2004), as well as the organisms studied. An example is metapopulation dynamics, which can be identified at various scales, but will depend upon the scale of distribution and the dispersal ability of the population (e.g., sessile vs mobile species) (Schowalter 2006). An issue still persists; the scale chosen remains arbitrary, and tends to reflect our own hierarchical perception of the environment (Wiens 1989, Levin 1992). Even though the size of the scale is biased, the ideal solution is to explore a wide array of spatial scales (Wiens *et al.* 1986), trying to get the most complete portrait possible of the ecosystem studied, since changes are taking place on several scales (Levin 1992).

Some recent studies have used a multi-scale perspective (e.g. Gering *et al.* 2003, Summerville *et al.* 2003a, Chandy *et al.* 2006, Gabriel *et al.* 2006). The number of scales varies from one study to another, but generally includes three to four scales that are often hierarchically nested, meaning that data present in one grain (the smallest) is enveloped into the next highest grain (Palmer and White 1994, Tokeshi 1999), presenting some scale dependency. A hierarchical approach provides insights into the effects of scale in ecological processes (Noda 2004). This allows identification of patterns across the nested spatial scales in order to detect variation between scales and a potential existence of non-random patterns at a specific scale.

Additive partitioning of species richness

Although diversity has been the subject of ecological studies for a long time, it is only recently that diversity has been partitioned into different components to allow it to be more easily combined with a scaling approach. Whittaker (1972) was among the first to split diversity into three components: α (local) diversity, β (between habitat) diversity and γ (in a range of habitats; e.g., landscape, geographic area, island) diversity. He used a multiplicative relationship between the three components, expressed by the equation $\beta = \gamma / \alpha$, which did not allow the direct comparison of the different components.

Allan (1975) examined hierarchical diversity and found that the sum of microhabitat diversity, site diversity and species diversity should equal total diversity (i.e., γ -diversity of Whittaker), thus moving toward an additive method. He also thought that this partitioning approach could be useful to compare diversity among different assemblages (e.g., tropical versus temperate diversity). Without using the same terminology as Whittaker (1972), Allan split the components in a similar way: a micro-habitat component (α_1), between microhabitats (β_1), within site component (α_2) and between sites (β_2), indirectly including a scaling approach.

Lande (1996) modified the approach of Whittaker as an additive partitioning approach using the original terminology but in an additive method instead, where $\gamma = \alpha + \beta$. In this case, the total species diversity (regional pool, i.e. γ diversity) of a community can be partitioned into additive components within (α -diversity) and among (β -diversity) communities. Having the same units, the different elements of the equation can be directly compared. However, the relationship between α and β is scale dependent (Ricklefs and Schluter 1993, Magurran 2004); their contribution to γ -diversity will vary with the spatial scales chosen. This framework allows diversity to be measured with different levels of organization, or across different scales: $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3$ (Wagner *et al.* 2000, Gering *et al.* 2003). It allows the actual number of communities to be estimated by extrapolating the partitioned observed species diversity of a randomly chosen community (Lande 1996). This approach might also give insights into understanding the saturation of communities, more than the local-regional richness curves that were previously used (Loreau 2000). Studies that partition diversity have multiplied in recent years, and some have focused on improving methodology (e.g. Crist and Veech 2006), testing null hypothesis (Crist et al. 2003) or showing the utility of the alpha-beta-regional (ABR) approach compared to the older local-regional approach (Gering and Crist 2002). Partitioning of diversity has been used to identify patterns of species diversity in forest arthropods (e.g. Gering and Crist 2000, Gering et al. 2003, Summerville et al. 2003a, Summerville et al. 2003b, Novotny and Weiblen 2005, Summerville and Crist 2005, Novotny et al. 2007, Lindo and Winchester 2008, Ribeiro et al. 2008), in plants (e.g. Wagner et al. 2000), in agricultural fields (e.g. Gabriel et al. 2006, Clough et al. 2007, Diekötter et al. 2008), in reefs (e.g. Rodriguez-Zaragoza and Arias-Gonzalez 2008), and to test effects of fragmentation on beetles (Fournier and Loreau 2001) and the effect of organic farming on butterflies (Rundlöf et al. 2008). Most of these studies focused on the use of additive partitioning across different spatial scales. This approach allows conservation biologists to understand the contribution of α - and β -diversity to total diversity over a range of user-defined spatial scales (Gering *et al.* 2003). In addition, the partitioning of diversity allows a focus on the protection of regionally distinctive species assemblages and on natural dominant patterns (Summerville et al. 2003a).

Diversity patterns in forest arthropods

Some recent studies have focused on diversity patterns through a range of different scales, using forest arthropods as study taxa, in order to give potential insights into the ecological processes underlying these patterns. Gering and Crist (2000) studied patterns of host-tree differences, spatial variation, and temporal change among canopy beetle (Coleoptera) communities in temperate deciduous forest (beech-sugar maple) in Ohio. They concluded that richness and diversity differed more with increasing spatial scales, and that one study plot is limited in explaining broader biogeographic patterns of insect distribution. Gering *et al.* (2003) went a step further by considering the scale dependency on diversity, using additive partitioning to study which spatial scales (i.e., tree, stand, site and

ecoregion) most strongly influence the diversity of canopy beetles in southern Ohio and Indiana. They partitioned the diversity, not only among the scales, but also by comparing diversity of rare and common species to the entire community. They showed that patterns not only changed across scales but also across different subsets of species, rare species accounting for a higher proportion of diversity between ecoregions, while common species were contributing more at smaller scales (i.e., tree level: α -diversity).

More studies have focused on diversity patterns of Lepidoptera, such as Summerville et al. (2003a) who studied moths in temperate forests in Ohio, using a similar protocol to Gering et al. (2003). However, they used only three scales (i.e., stand, site and region) to study the variation of moth diversity and community composition. They found that each spatial level contributed a proportion of unique species to the community, that their composition was mostly influenced by broader scale, represented by a large number of unique species for each ecoregion, while species dominance and evenness were more driven by finer spatial scales. Instead of additive partitioning through a scaling approach, Summerville *et al.* (2003b) used β -diversity to compare the community structure of arboreal Lepidoptera caterpillars across four tree species in eastern deciduous forest in Ohio. By comparing among tree individuals and tree species, they found that oaks supported greater species richness and abundance than American beech. Fewer caterpillars were also restricted to a single host, while many species were limited in terms of spatial distribution within a forest. Summerville et al. (2008) determined the spatial patterns of Lepidoptera at the stand and the watershed scale in forest patches in three Midwest watersheds. Species richness did not differ among watersheds or among forest stands. However, the stand was the scale contributing the most to diversity.

DeVries *et al.* (1999) examined the diversity of fruit-feeding butterflies at multiple spatial and temporal scales in Ecuador, finding significant differences (β -

diversity) in species composition in regard to height, area and sampling period. Ribeiro *et al.* (2008) determined the diversity of fruit-feeding butterflies in fragmented landscapes of the Brazilian Atlantic Rain forest, where they also verified their distribution across scales (i.e., trap, fragment and landscape). Butterflies were not randomly distributed inside forest fragments, probably due to intraspecific aggregation at a small scale. They also recognized that the next step is to investigate the processes that drive these spatial patterns.

Lindo and Winchester (2008) examined oribatid mite communities between canopy suspended soil and forest floor soil in temperate rainforest of British Columbia, by partitioning diversity through a nested hierarchical scaled design (i.e. core, patch and tree). Species richness and abundance were higher on the forest floor. However, the canopy mites had more limited dispersal, corresponding to high β -diversity at the tree level. They acknowledged, though, that more factors might be limiting the distribution of mites, since β -diversity was also high at patch and tree level for the forest floor mites. Larrivée (2009) investigated the community composition and species richness of spider assemblages in Quebec forests across multiple scales (i.e., tree, stand, site and region), but also tried to find the processes explaining these patterns. Spider assemblages were significantly different between understorey and canopy, as well as at stand and site level. The β -diversity at the site level was higher than expected, indicating spatial aggregation of the conspecifics. Larrivée concluded that the ecological processes controlling spider assemblages were most likely species-sorting dynamics at small scales (tree and stand), and patch-dynamics and mass-effects at larger scales (site and region).

Although community ecology studies using Diptera are few, Stireman (2008) examined diversity patterns over space (i.e. trap and habitat) and time in a tachinid parasitoid community in oak-mesquite savanna in Arizona. Tachinid species richness (79 species) was fairly high considering the small area covered

(~1-2 ha), which indicates a rich fauna of tachinid flies in that region. β -diversity was high among microhabitat types and sampling dates, explaining 73% and 43%, respectively, of the total diversity. These patterns likely reflect differences among the tachinid species regarding their host range, but could also be affected by the presence of site-specific mating areas. The latter might account for a large part of β -diversity between microhabitat, since males were overrepresented in the canopy traps and underrepresented in open traps. On the other hand, bimodal precipitation in the region might account for the higher differences among sampling dates.

Diptera diversity

Diptera (true flies), have received little attention in studies of diversity in forests, compared to beetles and moths. Nevertheless, Diptera are the fourth most diverse order of insects, representing up to 10-15% of known animal species (Brown 2005, Grimaldi and Engel 2005, Yeates and Wiegmann 2005) with an estimated 153,000 described species worldwide (Pape et al. 2009). The real number of species might be as high as one million (Hammond 1992, Brown 2001). In Canada, Diptera is the largest order, comprising approximately one-quarter of the insect fauna and outnumbering the Coleoptera (Danks 1979). More than 7,000 species of Diptera have been recorded in Canada, and it has been estimated that about the same number of species is present but undescribed or unrecorded (Danks 1979). Diptera is one of the least studied of the megadiverse orders (Brown 2005), and tend to be ignored by many entomologists and ecologists (Disney et al. 1982, Disney 1986). Not a single habitat has a complete comprehensive list of the dipteran fauna (Disney 1986). This might be partly explained by the taxonomic challenge they represent (Langor et al. 2008), the taxonomic impediment – too few specialists for too many species (Giangrande 2003) or by the lack of appeal of most Diptera to amateur entomologists compared to groups such as butterflies (Grimaldi and Engel 2005). The lack of taxonomic, faunistic and ecological knowledge makes Diptera a challenging prospect for comprehensive biodiversity inventories (Thompson 2009).

The group of interest in this study is the Schizophora, a large, ubiquitous group of flies that is exceptionally diverse (Grimaldi and Engel 2005). It is a subsection of Diptera, included in the infraorder Cyclorrhapha, the higher flies (Brown 2001, Grimaldi and Engel 2005). Schizophora is further split into two subgroups: the Acalyptratae and the Calyptratae, together these groups account for about 50,000 described species worldwide (Grimaldi and Engel 2005) and about 7,600 (~3,900 Acalyptratae; ~3,700 Calyptratae) for the Nearctic region, distributed in 61 families (Thompson 2009). However, the estimated total number of species for the Nearctic region is twice as high (Thompson 2009). This high diversity comes largely from a handful of species-rich families. In the Calyptratae, four families (Tachinidae, Anthomyiidae, Muscidae, Sarcophagidae) account for over 87% of the Nearctic species (Thompson 2009). Six families (Agromyzidae, Tephritidae, Chloropidae, Sphaeroceridae, Drosophilidae, Ephydridae) account for over 64% of the Nearctic species of Acalyptratae (Thompson 2009). In Canada, about 3,000 species of Schizophora have been reported and many more remain unrecorded or undescribed (Danks 1979).

Studies on forest Diptera

Diptera are the most ecologically diverse groups of insects (Grimaldi and Engel 2005, Kitching *et al.* 2005, Yeates *et al.* 2007), and are often among the most abundant animals collected in temperate habitats (Hughes *et al.* 2000), wetlands (Hansen and Castelle 1999), forests (Stork 1988, Yamashita and Hijii 2007), freshwater (Wagner *et al.* 2008) and carrion (Watson and Carlton 2003). Their high abundance allows a great number of specimens to be collected, increasing the robustness of statistical analyses (Kitching *et al.* 2004). The high ecological diversity of Diptera makes them a more representative indicator of the richness of the ecosystem (Disney 1986), compared to assessment using more ecologically restricted orders such as Lepidoptera (~90.9% phytophagous) (Kitching *et al.* 2005). Diptera can be good model taxa and should be of particular interest in diversity and ecology studies, due to their ubiquity, their fine scale habitat requirements (Deans *et al.* 2007), their importance in the ecosystem (e.g.,

pollinators, decomposers, natural enemies, role in food webs) (Danks 1979), their high abundance and diversity. Despite that, Diptera remain rarely used in biodiversity studies.

While Diptera have been partly inventoried in some ecosystems (e.g., grasslands: Boucher and Wheeler 2001, Crecco 2001, Lambkin *et al.* 2008; wetlands: Hansen and Castelle 1999, Keiper *et al.* 2002, Foote 2004, 2007, Beaulieu and Wheeler 2005, Schimitz *et al.* 2007), studies focusing on forest Diptera have been limited. In most cases, these studies have focused on a specific guild or family, limiting the survey's range. An exception was Fast and Wheeler's (2004) faunal inventory of Brachycera (higher flies) in a southern Quebec old growth forest, which collected more than 334 species from May to September.

The saproxylic guild has been the most extensively studied group of forest Diptera, since they may constitute up to 80-90% of the insects reared from dead wood (Økland 1996). Some studies have examined the diversity of saproxylic Diptera (Rotheray et al. 2001) and others their abundance in different types of decaying wood (Hövemeyer 1998). Selby (2005) focused on the diversity of a single dominant family, the Cecidomyiidae, in a Quebec beech - sugar maple forest and found that logs in advanced stages of decay are more species-rich than younger logs. The two other most species-rich and abundant families in dead wood are Sciaridae and Mycetophilidae (Hövemeyer and Schauermann 2003), the latter being among the most important mycophagous insect families (Økland 1996, Økland et al. 2005, Yamashita and Hijii 2007). The diversity of Mycetophilidae has been studied in oak (Økland et al. 2005) and spruce forests (Økland 1996), where they represented 88% and 92%, respectively, of the species richness found. The fungivorous diversity of dipteran species (i.e. Tipulidae, Phoridae, Platypezidae, Chloropidae, Drosophilidae), reared from mushrooms has been investigated (Bunyard 2003), as well as that of saproxylic Syrphidae (Reemer 2005).

Other non-saproxylic Diptera families have also been studied in forests. The community structure and species composition of Phoridae has been studied in association with habitat degradation (Durska 1996), and secondary succession in pine forest (Durska 2001). Tachinidae species composition in different forest habitats has also been explored (Belshaw 1992), as well as Calliphoridae diversity, which is limited in forest (i.e. ten species) (Marinho et al. 2006). Syrphidae have been inventoried in broadleaf-pine forests (Fritzler et al. 2006) and their sensitivity to harvesting and potential as indicator species investigated (Deans et al. 2007). Drosophilidae are abundant in forests, and they are more widely studied than many other families. Drosophilid phenology has been explored for temporal changes (Benado and Brncic 1994, Argemi et al. 1999), but also for vertical distribution (Tidon-Sklorz and Sene 1992). All of these studies found an influence of climatic conditions on population fluctuations, although their potential as indicator species for climate change was not as clear (Parsons 1991). Toni et al. (2007) studied the drosophilid assemblage in mainland and island forests and found evidence for the importance of the spatial component in structuring communities

Flies are among the most abundant members of the soil insect community (Frouz 1997, 1999, Hövemeyer 1999a, b) and, as a result, soil Diptera have been the focus of some studies. Most of the species found in this habitat are only temporary residents (Nielsen and Nielsen 2004, 2007), using soil as a substrate for their pupariation, pupation or hibernation (Hövemeyer 1991), although several others spend most of their life there for larval development.

Despite those above examples, studies on forest Diptera ecology remain rare and scattered, especially in North America (Bunyard 2003, Fast and Wheeler 2004, Selby 2005, Deans *et al.* 2007).

Objectives:

The increased focus on community ecology of insects has generated several new questions in recent years. It is still not known, for example, if the assemblages of Diptera in local habitat patches are predictable, or are just random sets of species. And if there is an obvious pattern, at what scale does it become apparent? To answer that question, I used the additive partitioning approach to determine the nested patterns of β -diversity in temperate forest Diptera, focusing on the Schizophora, and using three different spatial scales (i.e., tree, stand and site). The principal objectives of this study were: 1) To determine α -, β - and γ -diversity of Schizophora in temperate deciduous forests, to determine their nested patterns of β -diversity, and the scale contributing the most to species richness. 2) To verify at the different spatial scales if the patterns of diversity differ between different subgroups of Schizophora; namely, rare versus common species and Acalyptratae versus Calyptratae.

Hypotheses and predictions Hypothesis 1:

 β -diversity will be low at the smallest scale (tree level), and high at the two largest scales (stand and site level) because of isolation and low dispersal ability of the species present. If the stand level corresponds to the local community size, it will be the scale contributing the most to diversity.

Hypothesis 2:

Rare species will have higher β -diversity at the largest scale (e.g., for a region or a site), since they are locally rare, while common species will have higher β -diversity at a small scale (tree level) due to their high local abundance and then be typical for a specific stand. Acalyptratae, being generally smaller in size, will have higher β -diversity at the tree level, while Calyptratae will have higher β -diversity at the stand level.

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CONNECTING STATEMENT

Diversity patterns, metacommunity dynamics and ecological processes have been found to vary across spatial scales. Since then, a scaling approach has been gaining in popularity in community ecology and diversity studies have been adapted to that approach by partitioning the diversity among the different scales used in order to quantify the variance in diversity patterns. Until now, this method has been applied to a variety of forest arthropods (i.e., beetles, moths, spiders and mites). However, Diptera have not been studied with that approach, despite the fact that they are among the most species-rich and ecologically diverse groups of arthropods in forests. The ecology of forest Diptera remains poorly known and studied in North America, as seen in Chapter 1. Chapter 2 builds on a small number of previous studies of Diptera diversity in Quebec forests and attempts to describe and quantify the diversity and ecology of forest Diptera by determining their diversity patterns at different scales in order to see if the assemblage is predictable or random.

CHAPTER 2: NESTED PATTERNS OF BETA-DIVERSITY IN FOREST DIPTERA

ABSTRACT

Are the assemblages of flies (Diptera) in local habitat patches predictable, or are they random sets of species? And if there is an obvious pattern, at what scale does it become apparent? The purpose of this study was to address these questions by describing the nested patterns of alpha-, beta-, and gamma-diversity in temperate forest Diptera, using the additive partitioning approach. The diversity patterns were studied by determining the alpha richness and the regional pool; the nested patterns of beta-diversity; and the scale contributing the most to species richness. Diversity patterns were also examined for two subordinate taxonomic groups (Calyptratae and Acalyptratae) and common versus rare species. Fieldwork was carried out in June-July 2008 in sugar maple stands in three southwestern Quebec forest fragments using three spatial scales (tree, stand, and site). Each site had four randomly selected stands, with six trees per stand, and two traps per tree. Dipteran species diversity (239 species) and composition was non-random at all scales selected, and varied across scales. These scales were not equally important across the different groups, as shown by the different diversity patterns. Smaller scales seem to structure Diptera species composition (β_1 : between trees), as well as the two taxonomic groups: Calyptratae and Acalyptratae. Common species were also more important at finer scales (α_1 : within trees), while rare species varied more at broader scales (β_3 : between sites). The scale contributing the most to γ -diversity was variable across the different groups, but β_1 was the overall trend, which was statistically supported by additive partitioning, NMDS, MRPP and similarity indices. Environmental variables weakly supported species composition for the regional pool, but at the site level, latitude, longitude and soil moisture had a more significant influence on assemblages.

INTRODUCTION

Arthropods are a major component of biodiversity in forests, often representing over half of the recorded species (Schowalter 2006). They are ecologically important, species rich and abundant, although their abundance varies dramatically between species. Despite their dominance in these ecosystems, forest arthropods remain poorly studied and little is known about the biology, distribution, diversity, vulnerability and conservation of most species (Norton 1996, New 1999, Hughes *et al.* 2000, Miller *et al.* 2008). Nevertheless, because of their diverse and dominant roles in forests a greater understanding of forest arthropod ecology is necessary in order to gain a more complete picture of the dynamics of forest ecosystems.

Assemblages of forest arthropods are usually made up of a few abundant species and a large number of rare species (Tokeshi 1999, Dajoz 2000). Rare species, represented by only one or two specimens, can comprise more than 30% of all specimens collected in samples (DeVries *et al.* 1999, Novotny and Basset 2000, Gering *et al.* 2003, Beaulieu and Wheeler 2005, Caterino 2007, Nielsen and Nielsen 2007, Ewers and Didham 2008).

Species abundance distributions (SAD) can be used to examine these species richness patterns (Magurran 2004) and determine the relative contribution of rare and common species. Furthermore, SAD can be constructed based on sampling at multiple scales, to dertemine differences in the contribution of rare and common species at different scales (Tokeshi 1999, Hirao *et al.* 2006).

Because diversity patterns are scale dependent (Levin 1992, Palmer and White 1994, Rosenzweig 1995, Leibold *et al.* 2004, MacNally *et al.* 2004), a multiscaling approach is important in detecting the most complete portrait possible of the ecosystem studied. Although, the importance of using a scaling approach in ecology has been emphasized previously (Wiens *et al.* 1986), it has been neglected in several studies (Schowalter 2006). A scaling approach allows identification of the actual dynamics and patterns, and not just artefacts arising from the use of a single scale (Wiens 1989). All species possess different habitat requirement and dispersal capacity (Novotny and Weiblen 2005, Cadotte 2006, Hirao et al. 2008b), and thus communities can exhibit heterogeneity at a variety of scales (Levin 1992, McLaughlin and Roughgarden 1993, Tokeshi 1993). Hence, the patterns detected will depend on the scales selected (Levin 1992, Palmer and White 1994, Rosenzweig 1995, Leibold *et al.* 2004, MacNally *et al.* 2004), as well as the organisms studied. Since changes are taking place on several scales (Levin 1992), the ideal solution is to explore a wide array of spatial scales (Wiens *et al.* 1986). Hierarchically nested scales allow testing for the optimal scale to detect the main processes acting on particular taxa in particular habitats.

Although diversity has been the subject of ecological studies for a long time, it is only recently that diversity has been partitioned into different components to allow it to be more easily combined with the scaling approach. Whittaker (1972) was among the first to split diversity into three components: α -, β - and γ -diversity. However, the relationship between the three component was multiplicative ($\beta = \gamma$ $/\alpha$), which did not allow the direct comparison of the different components. Allan (1975) moved toward an additive method, although he did not use the same terminology as Whittaker. Lande (1996) modified Whittaker's approach as an additive partitioning approach using the original terminology but in an additive method instead, where $\gamma = \alpha + \beta$. However, the relationship between α and β is scale dependent (Ricklefs and Schluter 1993, Magurran 2004); their contribution to γ -diversity will vary with the spatial scales chosen. By partitioning diversity into α , β and γ component, it allows direct comparison of the different elements (Lande 1996) and hence an understanding of the contribution of α - and β -diversity to total diversity (Gering et al. 2003), and to that of each scale selected (e.g., Wagner et al. 2000, Gering et al. 2003). Diversity partitioning also allows a focus on regionally distinctive species assemblages and on natural dominant patterns (Summerville et al. 2003a).

A number of studies of forest arthropods have examined diversity patterns at multiple scales. Taxa studied include canopy beetles (Gering and Crist 2000, Gering *et al.* 2003), Lepidoptera (DeVries *et al.* 1999, Summerville *et al.* 2003a, Summerville *et al.* 2003b, Ribeiro *et al.* 2008, Summerville *et al.* 2008), oribatid mites (Lindo and Winchester 2008) and spiders (Larrivée 2009).

There have been no similar studies on Diptera, despite the fact that flies are the most ecologically diverse groups of insects (Kitchings and Walton 1991, Grimaldi and Engel 2005, Kitching *et al.* 2005, Yeates and Wiegmann 2005, Yeates *et al.* 2007), and are often among the most abundant animals collected in forests (Stork 1988, Hughes *et al.* 2000, Yamashita and Hijii 2007). Their high abundance allows the collection of a great number of specimens for studies, increasing the robustness of statistical analyses (Kitching *et al.* 2004). The high ecological diversity of Diptera makes them a more representative indicator of the richness of the ecosystem (Disney 1986), compared to assessment using more ecologically restricted orders such as Lepidoptera (~90.9% phytophagous) (Kitching *et al.* 2005). Because of their ubiquity, their fine scale habitat requirement (Deans *et al.* 2007), their importance in the ecosystem (e.g., pollinators, biological control agents, links in food web) (Danks 1979), their high abundance and diversity, Diptera should be more widely used in biodiversity studies.

Diptera have received little attention in forest diversity studies in North America and most have focused on single taxa or microhabitats. Selby (2005) studied the diversity of saproxylic Cecidomyiidae in decaying deciduous logs in southern Quebec. Deans *et al.* (2007) examined the sensitivity of Syrphidae to forest harvesting in the boreal forest. Bunyard (2003) reared mycetophagous Diptera in several families from fungi in Ohio. Fast and Wheeler (2004) covered a broader range of Diptera taxa in a faunal inventory of Brachycera in a southern Quebec deciduous forest, identyfing 334 species. However that study was restricted to a single site. The group of interest in this study is the Schizophora, a large, ubiquitous group of flies that is exceptionally diverse (Grimaldi and Engel 2005). It is a subsection of Diptera, included in the infraorder Cyclorrhapha, the higher flies (Brown 2001, Grimaldi and Engel 2005). Schizophora is further split into two subgroups: the Acalyptratae and the Calyptratae; together these groups account for about 50,000 described species worldwide (Grimaldi and Engel 2005) and about 7,600 (~3,900 Acalyptratae; ~3,700 Calyptratae) for the Nearctic region, distributed in 61 families (Thompson 2009). In Canada, about 3,000 species of Schizophora have been reported and many more remain unrecorded or undescribed (Danks 1979).

Here we addressed the question of whether the assemblages of Diptera in local patches are predictable or just random sets of species; and if there is an obvious pattern, at what scale does it become apparent? To answer that question, the additive partitioning approach was used to examined nested patterns of betadiversity in temperate forest Diptera (Schizophora). The main objectives were: 1) To determine α -, β - and γ -diversity of Schizophora in temperate deciduous forest, to determine their nested patterns of β -diversity, and the scale contributing the most to species richness; 2) To verify at the different spatial scales if the patterns of diversity differ between different subordinate taxa of Schizophora (Acalyptratae versus Calyptratae) or between rare versus common species.

MATERIALS AND METHODS

Study sites and sampling design

This study was carried out in southwestern Quebec, using three of the Monteregian hills as study sites (Figure 2.1): Mont Saint-Bruno (45°33'0"N, 73°19'8"W), Mont Saint-Hilaire (45°33'7"N, 73°9'49"W) and Mont Rougemont (45°28'35"N, 73°3'17"W). The Monteregian hills are all Cretaceous-age igneous intrusions (Feininger and Goodacre 1995) that rise above the surrounding low-lying land. This common geological background influences the topography of the hills which, in turn, affects the flora and fauna. These hills represent small patches of forest in a matrix of suburban development and agricultural fields. The

dominant forest type at the sites is American beech (*Fagus grandifolia* Ehrh) – sugar maple (*Acer saccharum* Marsh) (Smith 1980). The isolation of the three hills and the similarity in their forest cover allowed them to be treated as distinct sites, and as replicates for the site level for this study.

Sampling was done using a hierarchical nested design (Figure 2.2) at three scales. The site level, represented by the hill, was the largest scale. Four stands, dominated by American beech and sugar maple, were selected at each site. Each stand was 60 m by 60 m, based on Chust *et al.* (2004) who found that 60 m was the optimal scale (i.e. explained most of the variance in species richness) for all species of Diptera in their study. Within each stand, six plots, 6 m by 6 m square, were selected and one healthy sugar maple with a diameter at breast height (DBH) of at least 10 cm was selected in each plot for sampling Diptera. This resulted in a total of 72 trees for the study. Stands and trees were randomly selected in the accessible area of the forest type at Mont Saint-Bruno and Mont Saint-Hilaire. At Mont Rougemont, stand selection was constrained by available access granted by private landowners, accounting for the smaller spacing between stands.

Diptera sampling and preparation

Sampling was conducted from 09 June to 22 July 2008 to cover the peak of adult Diptera activity in the region (see Fast and Wheeler 2004). Each tree was sampled using two traps. A trunk trap, consisting of a two litre soft drink bottle with the bottom removed, inverted and tied tightly against the trunk (Fast and Wheeler 2004) was used to collect insects walking on or flying near the trunk. A flight-intercept trap, consisting of a black vertical mesh panel 100 cm long by 75 cm high suspended just above ground level with a row of six yellow pan traps under the panel was also used to collect low-flying or crawling insects. Propylene glycol, diluted 1:1 with water, was used to preserve insects in the traps and a drop of liquid soap was used in each trap to break surface tension.

Traps were emptied once a week and the specimens transferred into 70% ethanol. Small specimens of higher Diptera were removed from sample residues, dried using Hexamethyldisilazane and mounted on points, while larger flies were dried using ethyl acetate and directly pinned. All Schizophora specimens were identified to species when possible using published taxonomic keys, or to morphospecies. All specimens are deposited in the Lyman Entomological Museum (McGill University, Ste-Anne-de-Bellevue, QC.).

Environmental variables

Environmental variables were measured using a two meter square quadrat on the north side of every tree sampled. Soil moisture was measured with a qualitative scale (0 = bare rock; 1 = cracking (very dry/sandy), 2 = dry soil, 3 = moist soil, 4= saturated soil, 5 = water table at surface). Litter depth was directly measured with a ruler, as well as the DBH. GPS coordinates and elevation were taken three times over the summer and averaged. Vegetation cover (i.e. litter, mosses, lichens, herbs, shrubs and trees) was assessed inside the quadrat using Braun-Blanquet scale (Goldsmith *et al.* 1986): 0 = <1%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 =51-75%, 5 = 76-100%. The same scale was used to measure the volume of dead wood (i.e., two categories: coarse and fine woody debris), while decay stages of the two categories of woody debris were assigned using Pyle and Brown's (1999) scale for hardwood (1 = bark firmly attached; 2 = wood solid, bark not firmlyattached; 3 = wood surface may flake off; 4 = kicked log may break into large pieces; 5 = 85% powdery wood). Plant diversity was measured in the quadrat of three randomly selected trees per stand, where all the dominant species were identified and then assigned to a class using the Braun-Blanquet scale. Other special characteristics of the area surrounding the tree or in the stands were noted as extra information (e.g., close to water bodies).

Statistical analyses

For each tree, the two types of traps were pooled, as were all weeks of collecting. Rarefaction curves were generated to account for sampling efficiency. Samplebased rarefaction was used due to the sample-based data from the traps, but also to report the natural levels of sample heterogeneity in the data (patchiness) (Gotelli and Colwell 2001). Sample-based data allow consideration of individualbased rarefaction, which is preferable when examining taxon richness, sampling effort and accumulation of individuals (Gotelli and Colwell 2001). Individualbased rarefaction reduces sample data to a common abundance level, allowing direct comparisons of the species richness of different communities (Magurran 2004). Individual-based rarefaction was used to compare species richness of the three sites and was performed with EcoSim 7.0 using 10,000 randomizations (Gotelli and Entsminger 2007). Because rarefaction curves and rarefied species richness were similar, observed species richness was used to compare sites and for subsequent analyses. Total estimated species richness was calculated using the non-parametric abundance-based coverage estimator (ACE), which is based on the abundances of species with 1-10 individuals, where the number of abundant species (>10 individuals) is added to complete the estimate (Magurran 2004). Sampled-based rarefaction and ACE were generated with EstimateS 8.0 using 10,000 randomizations (Colwell 2006).

Species abundance distribution (SAD) was used to examine the structure of the data set. The rank/abundance graph was tested for fit to three different models that are commonly used in describing community structure: log series, truncated log normal, and geometric series (Tokeshi 1993, Magurran 2004). These models were applied to the entire data set, and the closest match was then verified at the site level. For the log series model (Fisher *et al.* 1943), abundance classes were obtained with Log₂, while for the geometric series model, species were assigned a rank (i.e., the most abundant species becomes species rank 1). For the truncated log normal model, abundance data were transformed using Log₁₀, which was also used to assigned abundance classes; the truncation point was 0.5. A Kolmogorov-

Smirnov goodness of fit test was applied to verify the model fit between observed and expected distribution, using a confidence of P = 0.05 and P = 0.01 (Sokal and Rohlf 1995). To verify if the three sites had similar SAD, they were compared with each other on the basis of rank/abundance plots using the Kolmogorov-Smirnov two-sample test with confidence of P = 0.05 and P = 0.01 to compare with the expected D_{max} (Sokal and Rohlf 1995).

Additive partitioning was used to determine the diversity patterns among scales using the equation:

$$\gamma$$
 (total diversity) = α_1 (within trees) + β_1 (among trees) + β_2 (among stands) + β_3 (among sites)

based on Lande (1996) and Gering et al. (2003). The absence of difference between observed α - and β -diversity and a random distribution was treated as the null hypothesis. The random distribution was generated with 10,000 randomizations (individual-based with weighted data) using PARTITION 2.0 (Veech and Crist 2007). Statistical significance was then assessed by the proportion of null values that were greater (or less) than the actual estimate, given as a *P*-value. Species richness was used for the partitioning of the whole data set (Schizophora), as well as for rare/common species comparison and Acalyptratae/Calyptratae comparison. Species were categorized as rare and common based on Gering et al. (2003), where rare species represented <0.05% of the total number of individuals and common species >0.5% of the total. These limits are arbitrary and may not correspond to truly rare species, but rather to species rarely collected in a particular study. In this case, it allowed comparison of diversity patterns among species categorized by their abundance in samples. This might also reflect partly their true abundance, if traps were efficient enough in collecting the diversity present at the sampling site.

Non-metric multidimensional scaling (NMDS) ordination (Clarke 1993) was performed to determine potential groupings based on species composition. Prior to ordination, singletons and doubletons were removed and species abundance was log transformed, the latter was also applied to quantitative variables of the environmental variables matrix. The initial ordination was run with six axes and then re-run with the number of axes recommended in the conclusion. The final ordination was computed with three axes, using Bray-Curtis distance, 100 runs with real data and 200 Monte Carlo simulations. Two joint plots were generated, one to test if the environmental variables influenced the species assemblage of the whole data set, the second to test the influence of plant diversity using only the plots in which plant diversity was measured (i.e., half the plots). Environmental variables were also tested at the site level. The stand level could not be tested because no solution was generated in the ordination. Canonical Correspondence Analysis (CCA) was performed with 100 Monte Carlo simulations for the complete data set and at the site level, to obtain the percentage of variance explained by these variables. Stand level did not fit the requirement of CCA. Since no clear clustering was visible with the ordination, a multi-response permutation procedure (MRPP) (Mielke and Berry 2007) was used to verify if the sites and the stands were significantly different using pairwise comparison based on Bray-Curtis distance. Because MRPP cannot be applied at the smaller scale, trees were compared using the Bray-Curtis similarity index in EstimateS 8.0. NMDS and MRPP were performed with PC-ORD 4 (McCune and Mefford 2007).

RESULTS

Species diversity

A total of 5,957 individuals belonging to 27 families were collected from the Schizophora group, of which 5,871 were identified to species or morphospecies, representing a γ -diversity of 239 species (Appendix 1). Species richness and abundance between families were both skewed, with Muscidae (38 species), Anthomyiidae (25 species), Tachinidae (25 species), and Sphaeroceridae (24 species) representing about 47% of the total species richness, while Muscidae

(n=1580), Drosophilidae (n=1409), Sphaeroceridae (n=444) and Dryomyzidae (n=395) accounted for over 65% of the total abundance.

Because the main objective of the study was to examine overall patterns of diversity, the two trap types were pooled for analyses; there were, however, differences in the species collected by each trap type. Although the majority of species were collected in flight-intercept traps, some were primarily or exclusively collected in trunk traps. These included some of the more common species such as *Aulacigaster neoleucopeza* (97% of the individuals, i.e. 38), *Neophyllomyza gaulti* (95% of the individuals, i.e. 138) and *Phaonia fuscicauda* (100% of the individuals, i.e. 68). Some of the rarely collected species such as *Aulacigaster mealpinei*, *Philygria debilis*, *Periscelis annulata*, *Lonchaea* sp.1, *Fannia canicularis*, *Fannia nidicola*, and *Fannia* sp.1 were collected exclusively in trunk traps.

Of the species identified, 70 (29.3%) were represented by single specimens and 37 (15.5%) by doubletons (Table 2.1). Values of ACE estimated that 76% of the expected species richness for all the sites was collected, with individual site values ranging from 64% to 73% (Table 2.1). At the site level, Mont Rougemont had the most individuals and species collected, but Mont Saint-Hilaire had higher rarefaction estimated species richness (Table 2.1, Figure 2.3 A). The rarefaction curve for all sites pooled (Figure 2.3 B) and for the individual sites did not reach an asymptote (Figure 2.3 C), corresponding with the results of ACE. The cumulative species richness was similar between the sites with the exception of Mont Saint-Bruno, where species accumulation slowed as samples accumulated (Figure 2.3 C).

The species abundance distribution differed significantly from log series, truncated log normal and geometric series distributions (p < 0.01); the closest match was the log series model (Figure 2.4 A). At the site level, all differed significantly from the log series (p < 0.01), as with the entire data set (Figure 2.4

B). The SAD between sites did not differ significantly from each other (p < 0.01). This result is similar to the rarefaction curves, both indicating that sites were similar in terms of species accumulation and SAD.

Diversity patterns across spatial scales

In the additive partitioning the observed value of α -diversity was significantly lower than expected (p > 0.95) at all scales, while β -diversity at each level was higher than expected (p < 0.0001) with the exception of the rare species, for which only β_3 was significant (p < 0.05) (Table 2.2).

For the entire community, the scale contributing the most to diversity was the tree (β_1), accounting for 37% of the diversity (Figure 2.5). Calyptratae followed a similar pattern with β_1 representing 34.4% of the total diversity, while for the Acalyptratae, the most important scale was α_1 with 36.6% of the diversity, followed closely by β_1 with 35.1% (Figure 2.5 A). The proportion of Calyptratae and Acalyptratae in the community was similar, accounting respectively for 53% and 47% of the species richness (Table 2.2), and 43% and 57% of the total abundance.

When the entire community was broken down into common and rare species, trees (α_1) accounted for the majority of the species richness of common species (59.5%), while the site level (β_3), represented 60.3% of γ -diversity for the rare species (Figure 2.5 B). Rare species ($n \le 3$) were a major component of the community, accounting for over 50% of the species richness, while only 44 species (18%) were classified as common species ($n \ge 29$) (Table 2.2).

NMDS ordination was used to illustrate species assemblages among all trees sampled (Figure 2.6). The stress value was 18.679 for a three-dimensional solution and all axes together explained 75.4% of the variance in species composition (p < 0.005). No clear separation of clusters was visible for sites, which was not unexpected since all had the same forest type. Despite that, sites

were still loosely grouped. Environmental variables weakly explained the variance in species data (14.6%), with only latitude (cumulative $R^2 = 0.358$) and longitude (cumulative $R^2 = 0.430$) having some small association (Figure 2.7). Only one plant species had an association with Diptera composition, *Aralia racemosa* (Araliaceae) (cumulative $R^2 = 0.535$), which was only present in some quadrats at Mont Saint-Bruno. However, more variables were important at the site scale, explaining 28.8% of the variance at Mont Saint-Bruno, 32.6% at Mont Saint-Hilaire and 32.2% at Mont Rougemont. Latitude and longitude remained important factors for all sites with cumulative R^2 varying between 0.454 and 0.911, while longitude was dominant over latitude for Mont Saint-Hilaire ($R^2 = 0.911$) and the opposite for Mont Rougemont ($R^2 = 0.834$). Soil moisture was mostly important for Mont Saint-Bruno and Mont Saint-Hilaire ($R^2 = 0.724$).

All sites were significantly different (p < 0.000) based on MRPP and their chancecorrected within-group agreement (*A*) was normal for community ecology data, being all under 0.03. At the stand level, all pairwise comparisons were significantly different (p < 0.05); the *A* values were higher than at the site level, but all under 0.3, which is considered a fairly high value (McCune and Grace 2002). Overall at the tree level, trees were not very similar, which explains the high β -diversity at that scale. Only three pairs of trees had a similarity index over 0.6. Even within stands, the composition was variable with the exception of stand 1 at Mont Rougemont where the average index was 0.581, including two pairs of trees over 0.6.

DISCUSSION

Dipteran species diversity and composition was non-random at all scales selected, and varied across scales. These scales were not equally important across the different groups, as shown by the different diversity patterns. Smaller scales seem to structure Diptera species composition, as well as that of the two subordinate taxonomic groups: Calyptratae and Acalyptratae. Common species were also more important at finer scales, while rare species varied more at broader scales. The scale contributing the most to γ -diversity was variable across the different groups, but β_1 was the overall trend.

The Diptera community varied highly at smaller scales, supported by additive partitioning, NMDS, MRPP and similarity index. All these tests showed that trees where different from each other even within a stand, accounting for the highest species richness contribution (β_1) across scales. It seems that the tree itself or its surroundings, represent a suitable complete ecosystem for many flies (i.e., potentially the size of a local community), instead of the stand size as found by Chust et al. (2004). Their study, however, was not restricted to forest habitat and did not use a nested design. Dispersal should not be a major limiting factor at that scale, and in fact might have contributed to increased local coexistence (Cadotte 2006). Dispersal usually becomes the limiting factor at larger scales, determining the extent of β -diversity (Novotny and Weiblen 2005, Hirao *et al.* 2006), although it affects both α - and β -diversity (Hubbell 2001, Kneitel and Chase 2004). In fact, high dispersal ability tends to homogenize communities by decreasing β -diversity (Loreau 2000, Hubbell 2001, Gering and Crist 2002, Cadotte and Fukami 2005, Cadotte 2006), otherwise, it increases local diversity through rescue effects and source-sink effects (Cadotte and Fukami 2005, Cadotte 2006).

Diversity at the tree level might also be a consequence of niche size or trophic guild. Resource specialization is known to have a strong influence on β -diversity patterns for butterflies (MacNally *et al.* 2004) and true bugs (Diekötter *et al.* 2008). Several dipteran species, many of which are rare, use a variety of ephemeral and patchy small-sized food sources, such as dung, dead snails, fungi, dead animals and tree wounds (Shorrocks and Sevenster 1995, Tokeshi 1999, Papp 2002). The patchy distribution of these resources, and thus of the flies,

might be a contributing factor to the importance of the local scale (tree) (Tokeshi 1999). This can also be seen in the species collected primarily or exclusively by trunk traps, which include several rarely collected species, many of which are probably more locally restricted to the trunk. Larvae of *Aulacigaster* and *Periscelis*, for example, feed in tree wounds and adults are generally collected close to the larval substrate. On the other hand, individuals of these species may have to disperse more to find those ephemeral resources (Schowalter 2006), which might partly explain the homogeneity between sites.

The patchy distribution of these ephemeral resources might explain the fact that α -diversity was the only partition that was lower than expected. Individuals within species have a tendency to aggregate together (Tokeshi 1999, Veech *et al.* 2003, Schowalter 2006), which is known to decrease α -diversity and inflate β -diversity (Veech *et al.* 2003, Veech 2005). This phenomenon might be accentuated by behaviour or by the patchiness of resources, forcing conspecific individuals to aggregate more. It can also result from sampling effects (i.e. traps) (Schowalter 2006) or from local extinction rates, influenced by local interactions, emigration rate and the composition of the species pool (Noda 2004).

In contrast, all β -diversity levels were higher than expected, which might be a consequence of co-occurrence, explained by the coexistence of species together. Species coexistence might be a ruling factor for flies. They tend to be locally aggregated, which promotes coexistence by increasing intraspecific competition, while reducing interspecific competition (Shorrocks and Sevenster 1995, Tokeshi 1999). They are ecologically diverse (Kitchings and Walton 1991, Grimaldi and Engel 2005, Kitching *et al.* 2005, Yeates and Wiegmann 2005, Yeates *et al.* 2007), and they have a wide range of sizes, which allows them to fill more diverse and small niches than species of other orders of insects (e.g., Coleoptera and Lepidoptera). Furthermore, habitat heterogeneity increases with scale (Gandhi *et al.* 2007), leading to an increase in niche availability and consequently increasing

coexistence (Tokeshi 1999, Schowalter 2006) and diversity (Tokeshi 1999, Wagner *et al.* 2000, Fournier and Loreau 2001, Brown *et al.* 2007, Diekötter *et al.* 2008). Small-scale disturbance and fragmentation, such as windthrow disturbance, might have contributed to stand level richness (β -diversity) through higher habitat heterogeneity. Diptera are susceptible to windthrow disturbances, decreasing their occurrence, at scales slightly larger than our stand size (i.e. 90 m radius) (Hirao *et al.* 2008). This might account for the high difference between the stands, since windthrow was an active disturbance (several storms over the collecting season) that affected stands in this study. However, the effect of habitat heterogeneity might have been limited by dispersal ability, which also affects coexistence, mainly through competition (Tokeshi 1999). As seen before, sites were more homogeneous probably partly due to resource specialization. Only a few species were site-specific, most of them were probably widely distributed across the region, but with patchy occurrence, accounting for the higher β -diversity between trees and stands.

Calyptratae and Acalyptratae followed a similar pattern to the regional pool, with all scales significantly different than expected. However, only Calyptratae had the tree scale as the main contributor to γ -diversity, while it was α_1 (within tree diversity) for the Acalyptratae. Acalyptratae are usually smaller flies (Marshall 2006) and tend to have smaller niche size. Several species are dependent on small-sized food and breeding resources that are ephemeral and unpredictable (Papp 2002). Thus, it is not surprising that they were more locally rich than Calyptratae. Calyptratae seem to be driving the entire community pattern more than the Acalyptratae, which might be reflected by their higher species diversity, although Acalyptratae were more abundant.

Common and rare species had clear and distinct diversity patterns. Common species were more locally abundant and diverse (α_1), while rare species were more specific at the site scale (β_3), represented by their usually patchy spatial

occurrence (Tokeshi 1999). Their relative proportion in the overall assemblage is usually linked with their dispersal ability and habitat requirements (Hirao *et al.* 2006), in this case, being influenced more at site scale. This picture is representative of insect surveys: few abundant and numerous rare species (Colwell and Coddington 1994, Dajoz 2000, Novotny and Basset 2000, Magurran 2004, Schowalter 2006, Nielsen and Nielsen 2007, Wilson *et al.* 2007). This explains the closer match with the log series model, which assumes high proportions of rare species (Tokeshi 1999, Magurran 2004, McGill *et al.* 2007). Rare species come generally from sampling at broader scales (Gering *et al.* 2003), where they are more likely to be encountered (Gabriel *et al.* 2006, Hui 2008). This may explain why rarefaction and accumulation curves rarely reach an asymptote, as in this study. Because of the increasing number of rare species at increasing scales, the saturation of the species accumulation curve is difficult to obtain even with extensive sampling.

Environmental variables did not explain much of the pattern at the regional pool scale but more at the site, where latitude and longitude were the most important along with soil moisture. Partitioning of diversity has shown that the Diptera community is more structured at smaller scales, which may explain the relationship of latitude and longitude with species composition in this study. However, the apparent effect of latitude and longitude may simply be an artefact arising from the fact that the three sites are arranged along a latitudinal and longitudinal gradient but the species assemblages differ for other reasons unrelated to the measured environmental variables. On the other hand, soil moisture probably has a greater influence on particular trophic guilds, such as saprophagous flies feeding in litter and woody debris and fungivores. Plant composition is known to be a good predictor for arthropods (Schaffers et al. 2008), but did not seem to influence the flies composition in this study. This may be explained by the fact that many of the Diptera species collected are neither primarily phytophagous, nor are predaceous or parasitic on other phytophagous species. The large number of saprophagous species might be influenced more by

45

dead than living plant material, and even the predaceous and parasitic species may be generalists, or feed on generalists.

The diversity pattern of the Diptera community differed from those in other arthropod studies in temperate forests, which were mostly dictated by larger scales. Canopy beetles, per example, were more structured at broader scales by ecoregions (Gering et al. 2003), while the patterns of common and rare species were more similar to Diptera although not as pronounced (i.e. Coleoptera had a bigger contribution of α_1 and less of the higher scales for common species, and Diptera higher β_3 for rare species). For both studies, the entire community was not random at all scales and had lower than expected α . Lindo and Winchester (2008) found a different pattern for oribatid mites, where only the two broader scales were not random (β_2 and β_3), the community being structured by the broader scale (i.e. for mite size $:\beta_3 =$ tree), as for canopy beetles. Larrivée (2009) found that broader scales also structured spider assemblages (both canopy and understorey), however, the only significantly different scale was the site (β_3) , which was the biggest contributor to γ -diversity. For moths, only sites (β_2) were significantly different than expected, although the within stands scale (α_1) contributed the most to richness, which was only significant for the late season (Summerville et al. 2003a). The moth community appeared to be influenced by broader scales, despite the lack of significance for the site level (β_2) (Summerville *et al.* 2003a).

This study has shown that diversity patterns change across spatial scales, justifying the importance of a scaling approach, but that these patterns also differ from taxon to taxon (flies, beetles, mites, spiders, moths), even in similar habitats and at similar spatial scales. This is not surprising, since detected α - and β -diversity patterns were dependent on many ecological factors, such as local dynamics, dispersal, habitat isolation, habitat heterogeneity and quality (Levin 1992, Tokeshi 1999, Gering and Crist 2002, Noda 2004), but also upon life history characteristics such as niche-breadth (Ricklefs 2004, Summerville *et al.*

2006). This study has also shown the relevance of rare species at broader scales, and, in this particular case, their contribution to differences between sites.

Just as patterns of diversity differ between different taxonomic groups, the processes explaining species composition might be potentially taxon-specific. For the Diptera, more ecological studies will be needed at smaller scales to determine which environmental factors explain their distribution and community composition. Further study of trophic guild patterns might be helpful in understanding the structure of fly assemblages. These data will be required to make inferences about the processes underlying the patterns. It would be interesting to examine the turnover rate of Diptera species in time, to verify the changes in diversity patterns throughout seasons and years, in order to see if they differ from the turnover in space. It would also be interesting to test the effect of habitat heterogeneity on dispersal as Freestone and Inouye (2006) did with plants. This could allow examination of to what extent the pattern of diversity may change over gradually increasing habitat heterogeneity.

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Table 2.1: Number of individuals, raw species richness (S_{obs}), rarefied species richness ($S_{rar} \pm SD$, standardized at 1700 individuals), mean ACE value and number of singletons and doubletons of Schizophora at Mont Saint-Bruno (B), Mont Saint-Hilaire (H), Mont Rougement and all sites pooled.

Sites	Ν	Sobs	S _{rar}	ACE	singleton	doubleton
В	1767	139	135.26 ± 1.28	191.54	45	19
Η	1739	157	155.62 ± 1.13	245.85	61	24
R	2365	163	143.97 ± 3.69	252.59	61	21
All	5871	239		314.65	70	37

Table 2.2: Additive partitioning results of α and β -diversity components across scales for the entire community and for each group (Calyptratae/Acalyptratae; Common/Rare species), presenting the average richness value obtained within each spatial scale and the total richness (γ).

	Entire	Calyptratae	Acalyptratae	Common	Rare
	community			species	species
γ	239	126	113	44	126
β3	6.6**	8.2**	3.3**	0**	76*
β2	80.0**	40.8**	28.6**	0.6**	34.6
β1	88.5**	43.3**	39.7**	17.2**	12.4
α1	63.9***	33.7***	41.4***	26.2***	3***

* Represents significantly different than expected (significantly higher than expected: * p<0.05, ** p<0.0001; significantly lower than expected: *** p>0.95). Significance value is based on the expected values generated with 10,000 randomizations with PARTITION software.



Figure 2.1: Location of study sites southeast of Montreal, Quebec, Canada (B: Mont Saint-Bruno, H: Mont Saint-Hilaire, R: Mont Rougemont. Inset shows arrangement of stands (1-4) within each study site.



Figure 2.2: Diagram of the hierarchical nested sampling design.


Figure 2.3: A) Individual-based rarefaction curve for Mont Saint-Bruno (B), Mont Saint-Hilaire (H) and Mont Rougemont (R) (\pm SD); B) sample-based rarefaction curves for all sites combined (\pm SD); C) sample-based rarefaction curve for Mont Saint-Bruno (B), Mont Saint-Hilaire (H), Mont Rougemont (R) and all sites combined (\pm SD) to represent the sampling efficiency.



Figure 2.4: Observed species abundance distribution versus expected values for log series distribution using a Kolmogorov-Smirnov goodness of fit with p < 0.01, for all the sites pooled (A) and for each site separately (B). B – Mont Saint-Bruno; H – Mont Saint-Hilaire; R – Mont Rougemont.



Figure 2.5: Percentage of species richness explained by α and β -diversity across the different scales for the entire community compared to Calyptratae and Acalyptratae (A) and compared to common and rare species (B). Total species richness for each group is represented at the top of the bar.



Figure 2.6: Non-metric multidimensional scaling ordination of Schizophora species composition of the 72 trees at Mont Saint-Bruno (B), Mont Saint-Hilaire (H) and Mont Rougemont (R). The two strongest axes of the three-dimensional solution are shown with the *P*-value and R^2 of each axis.



Figure 2.7: NMDS ordination from Figure 2.6 with joint plot of environmental variables, showing latitude (Lat) and longitude (Longi) vectors with their cumulative R^2 (for the 3 axes), using a cut-off at $R^2 = 0.200$.

Family	Species		Specimens		
		В	Н	R	
Acalyptratae					
Micropezidae	Rainieria antennaepes Say	52	5	5	62
Lonchaeidae	Lonchaea sp.1	0	3	0	3
	Lonchaea sp.2	1	1	0	2
Platystomatidae	Rivellia sp.1	2	2	2	6
Piophilidae	Protopiophila latipes Meigen	0	0	1	1
Clusiidae	Clusia czernyi Johnson	0	1	0	1
	Clusia lateralis (Walker)	4	5	3	12
	Clusiodes ?apiculatus Malloch	0	1	3	4
	Clusiodes johnsoni Malloch	0	10	5	15
	Sobarocephala atricornis Sabrosky & Steyskal	2	1	4	7
	Sobarocephala dreisbachi Sabrosky & Steyskal	3	3	11	17
	Sobarocephala lachnosternum Melander & Argo	0	0	3	3
	Sobarocephala latifrons (Loew)	34	55	122	211
Agromyzidae	Cerodontha dorsalis (Loew)	0	1	0	1
	Japanagromyza viridula (Coquillett)	0	2	0	2
	<i>Ophiomyia</i> sp.1	1	0	0	1
Aulacigastridae	Aulacigaster mcalpinei Mathis & Freidberg	3	1	1	5
	Aulacigaster neoleucopeza Mathis & Freidberg	9	11	19	39
Periscelididae	Periscelis annulata (Fallén)	1	2	2	5
Asteiidae	Leiomyza curvinervis (Zetterstedt)	1	0	1	2
Milichiidae	Neophyllomyza gaulti Brochu & Wheeler	30	28	87	145
	Neophyllomyza quadricornis Melander	2	4	5	11
	Paramyia nitens (Loew)	18	96	14	128
Dryomyzidae	Dryomyza anilis Fallén	8	26	10	44
	Dryomyza simplex Loew	91	186	74	351
Sciomyzidae	Limnia ?boscii (Robineau-Desvoidy)	0	0	1	1
	Limnia ?loewi Steyskal	0	1	5	6
	Sciomyza aristalis (Coquillett)	0	1	0	1
	Tetanocera canadensis Macquart	0	0	1	1
	Tetanocera valida Loew	0	29	31	60
	Trypetoptera canadensis (Macquart)	0	2	22	24
Sepsidae	Nemopoda nitidula (Fallén)	1	1	1	3
Lauxaniidae	Homoneura fraterna (Loew)	1	2	1	4
	Homoneura incerta (Malloch)	6	4	3	13

Appendix 1: Schizophora species and morphospecies collected at Mont St-Bruno (B), Mont St-Hilaire (H) and Mont Rougemont (R).

	Homoneura pernotata (Malloch)	0	1	0	1
	Homoneura philadelphica (Macquart)	5	7	21	33
	Homoneura ?wheeleri Miller	4	2	1	7
	Melanomyza gracilipes (Loew)	12	0	2	14
	Minettia lobata Shewell	10	10	10	30
	Minettia lupulina (Fabricius)	0	0	1	1
	Minettia lyraformis Shewell	2	0	1	3
	Minettia obscura (Loew)	0	0	4	4
	Poecilolycia ?novaescotiae (Shewell)	0	5	2	7
	Poecilolycia sp.1	0	1	0	1
	Poecilolycia ?subserrata (Shewell)	2	3	1	6
	Poecilominettia puncticeps (Coquillett)	0	1	0	1
	Sapromyza hyalinata (Meigen)	0	1	1	2
Heleomyzidae	Allophyla laevis Loew	7	3	12	22
	Amoebaleria helvola (Loew)	3	0	0	3
	Suillia convergens (Walker)	0	0	2	2
	Suillia longipennis (Loew)	5	7	8	20
	Suillia nemorum (Meigen)	26	20	14	60
Chryomyidae	Gymnochiromyia concolor (Malloch)	2	0	1	3
Sphaeroceridae	Apteromyia claviventris (Strobl)	0	0	1	1
	Apteromyia newtoni Marshall & Roháček	0	1	0	1
	Aptilotus sp.1	0	0	1	1
	Coproica acutangula (Zetterstedt)	0	2	0	2
	Coproica ferruginata (Stenhammar)	2	6	2	10
	Coproica hirtula (Rondani)	1	0	1	2
	Dahlimosina hirsutiphallus Marshall	1	0	0	1
	Leptocera erythrocera (Becker)	8	9	8	25
	Lotophila atra (Meigen)	1	0	0	1
	Mesosphaerocera annulicornis (Malloch)	5	10	1	16
	Minilimosina parva (Malloch)	6	3	5	14
	Nearcticorpus canadense Roháček & Marshall	5	13	7	25
	Nearcticorpus pecki Marshall & Roháček	1	0	1	2
	Opalimosina mirabilis (Collin)	0	2	7	9
	Rachispoda limosa (Fallén)	0	0	2	2
	Spelobia bifrons (Stenhammar)	1	1	0	2
	Spelobia brevipteryx Marshall	9	0	17	26
	Spelobia clunipes (Meigen)	12	15	145	172
	Spelobia frustrilabris Marshall	0	2	4	6
	Spelobia luteilabris (Rondani)	2	2	9	13
	Spelobia ochripes (Meigen)	2	1	1	4
	Spelobia quinata Marshall	82	13	8	103

	Spelobia semioculata (Richards)	3	0	2	5
	<i>Spelobia</i> sp.1	0	0	1	1
Drosophilidae	Amiota sp.1	1	0	0	1
	Chymomyza amoena (Loew)	22	7	13	42
	Drosophila sp.1	41	32	28	101
	Drosophila sp.2	13	23	22	58
	Drosophila sp.3	45	24	43	112
	Drosophila sp.4	248	151	230	629
	Drosophila sp.5	1	0	0	1
	Drosophila sp.6	81	58	116	255
	Drosophila sp.7	0	1	0	1
	Drosophila sp.8	0	0	8	8
	Drosophila sp.9	44	28	64	136
	Scaptomyza graminum (Fallén)	16	19	29	64
	Stegana coleoptrata (Scopoli)	0	1	0	1
Ephydridae	<i>Diclasiopa</i> sp.	1	0	0	1
	Ditrichophora exigua Cresson	1	2	0	3
	Hydrellia notata Deonier	0	0	1	1
	Nostima approximata Sturtevant & Wheeler	1	0	0	1
	Philygria debilis Loew	0	1	1	2
	Scatella stagnalis (Fallén)	0	0	2	2
Chloropidae	<i>Fiebrigella</i> sp.1	1	0	0	1
	Gaurax ocellaris Sabrosky	0	0	1	1
	Gaurax pseudostigma Johnson	0	1	1	2
	Gaurax shannoni Sabrosky	1	0	1	2
	Gaurax sp.1	0	0	1	1
	Malloewia abdominalis (Becker)	0	1		1
	Malloewia nigripalpis (Malloch)	1	0	1	2
	<i>Meromyza</i> sp.1	1	0	0	1
	Oscinella sp.1	1	0	45	46
	Oscinella sp.2	0	0	10	10
	Rhopalopterum soror (Macquart)	0	2	1	3
	Thaumatomyia glabra (Meigen)	0	0	1	1
	Thaumatomyia grata (Loew)	0	6	0	6
	Tricimba lineella (Fallén)	2	1	0	3
	Tricimba melancholica (Becker)	2	4	2	8
	Tricimba trisulcata (Adams)	0	1	5	6
Calyptratae					0
Scathophagidae	Americina adusta (Loew)	0	0	1	1
	Megaphthalma sp.1	0	0	2	2

	Megaphthalma sp.2	0	1	0	1
	Neochirosia nuda (Malloch)	1	1	0	2
	Parallelomma sp.1	2	0	0	2
	Parallelomma vittatum (Meigen)	1	0	1	2
	Scathophaga hiemalis (James)	0	1	0	1
	Scathophaga stercoraria (Linnaeus)	0	0	1	1
Anthomyiidae	Anthomyia oculifera Bigot	3	6	2	11
	?Calythea crenata (Bigot)	0	0	1	1
	?Chirosia stratifrons (Huckett)	0	13	0	13
	Delia ?platura (Meigen)	4	9	19	32
	Eustalomyia festiva (Zetterstedt)	1	0	2	3
	Eustalomyia vittipes (Zetterstedt)	3	0	0	3
	Hydrophoria ?implicata Huckett	1	1	0	2
	Hydrophoria lancifer (Harris)	15	0	28	43
	Hydrophoria ?proxima Malloch	1	0	0	1
	<i>Hydrophoria</i> sp.1	0	4	4	8
	<i>Hydrophoria</i> sp.2	0	1	0	1
	<i>Hydrophoria</i> sp.3	0	0	2	2
	Hylemya alcathoe (Walker)	15	17	8	40
	?Lasiomma octoguttatum (Zetterstedt)	2	2	2	6
	Pegomya sp.1	2	1	1	4
	Pegomya sp.2	0	4	1	5
	Pegomya sp.3	8	3	34	45
	Pegomya sp.4	3	5	0	8
	Pegomya sp.5	2	0	0	2
	Pegomya sp.6	1	0	0	1
	Pegomya sp.7	11	4	0	15
	Pegomya sp.8	29	22	42	93
	Pegomya sp.9	0	0	1	1
	Pegomya sp.10	1	0	0	1
	Pegomya sp.11	2	0	1	3
Fanniidae	Fannia americana Malloch	0	0	2	2
	Fannia armata (Meigen)	4	0	0	4
	Fannia brooksi Chillcott	0	1	1	2
	Fannia canicularis (Linnaeus)	1	2	1	4
	Fannia corvina (Verrall)	1	1	1	3
	Fannia difficilis (Stein)	0	2	1	3
	Fannia fuscitibia Stein	0	1	0	1
	Fannia immutica Collin	2	0	0	2
	Fannia nidicola Malloch	0	0	4	4
	Fannia sp.1	2	1	0	3

	Fannia spathiophora Malloch	1	0	1	2
	Piezura graminicola (Zetterstedt)	5	15	1	21
	Piezura nearctica Chillcott	11	65	68	144
Muscidae	Azelia ?triquetra (Wiedemann)	3	4	7	14
	Coenosia ?compressa Stein	0	2	0	2
	Coenosia ?intacta Walker	24	32	23	79
	Coenosia ?nigritarsis (Stein)	9	52	65	126
	Coenosia sp.1	0	1	0	1
	Coenosia sp.2	0	2	1	3
	Eudasyphora cyanicolor (Zetterstedt)	1	1	2	4
	Hebecnema nigricolor (Fallén)	1	1	2	4
	Helina ?cinerella (Wulp)	100	118	92	310
	Helina ?exilis (Stein)	3	3	0	6
	Helina ?marguerita Snyder	0	0	1	1
	Helina ?pectinata (Johannsen)	13	16	25	54
	Helina ?uliginosa (Fallén)	0	1	0	1
	Macrorchis ausoba (Walker)	1	0	10	11
	Muscina assimilis (Fallén)	112	63	95	270
	Muscina pabulorum (Fallén)	10	3	1	14
	Muscina pascuorum (Meigen)	8	3	5	16
	Muscina stabulans (Fallén)	0	0	2	2
	Mydaea flavicornis Coquillett	1	0	5	6
	Mydaea impedita Stein	5	2	1	8
	Mydaea neglecta Malloch	68	41	56	165
	Mydaea obscurella Malloch	0	0	1	1
	Mydaea occidentalis Malloch	3	1	1	5
	<i>Mydaea</i> sp.1	1	0	0	1
	Phaonia ?aberrans Malloch	9	12	13	34
	Phaonia apicata Johannsen	47	40	100	187
	Phaonia ?solitaria Stein	4	5	20	29
	Phaonia ?azygos Malloch	0	2		2
	Phaonia bysia (Walker)	10	20	20	50
	Phaonia ?fuscana Huckett	63	4	7	74
	Phaonia ?fuscicauda Malloch	15	29	24	68
	Phaonia ?nigricans Johannsen	0	1	2	3
	Phaonia ?serva (Meigen)	0	0	1	1
	<i>Phaonia</i> sp.1	11	8	4	23
	Phaonia sp.2	0	1	0	1
	Phaonia sp.3	0	1	0	1
	Spilogona ?pacifica (Meigen)	0	1	1	2
	Spilogona ?torreyae (Johannsen)	0	0	1	1

Calliphoridae	Calliphora ?terraenovae Macquart	4	1	4	9
	Calliphora vicina Robineau-Desvoidy	1	0	5	6
	Calliphora vomitoria (Linnaeus)	1	8	30	39
	Lucilia illustris (Meigen)	1	0	0	1
	Lucilia mexicana Macquart	0	0	1	1
	Lucilia silvarum (Meigen)	0	2	0	2
	Melanomya (Opsodexia) ?bicolor (Coquillett)	0	2	3	5
	Pollenia labialis Robineau-Desvoidy	0	1	4	5
	Pollenia pediculata Macquart	25	0	0	25
	Pollenia rudis (Fabricius)	5	4	62	71
	?Trypocalliphora braueri (Hendel)	0	0	1	1
Sarcophagidae	Boettcheria bisetosa Parker	24	18	17	59
	Boettcheria latisterna Parker	3	2	3	8
	<i>Lepidodexia</i> sp.1	6	1	0	7
	Ravinia querula (Walker)	0	0	1	1
	Sarcophaga nearctica Parker	1	1	0	2
	Sarcophaga subvicina Rohdendorf	0	1	1	2
	Sarcophaga triplasia Wulp	10	4	4	18
Tachinidae	Tachinid sp.1	0	0	1	1
	Tachinid sp.2	0	0	1	1
	Tachinid sp.3	0	1	9	10
	Tachinid sp.4	0	1	0	1
	Tachinid sp.5	1	0	0	1
	Tachinid sp.6	1	1	0	2
	Tachinid sp.7	4	1	0	5
	Tachinid sp.8	1	1	0	2
	Tachinid sp.9	0	1	0	1
	Tachinid sp.10	0	0	1	1
	Tachinid sp.11	0	1	0	1
	Tachinid sp.12	0	2	1	3
	Tachinid sp.13	0	1	0	1
	Tachinid sp.14	0	1	0	1
	Tachinid sp.15	1	0	2	3
	Tachinid sp.16	0	2	0	2
	Tachinid sp.17	5	35	25	65
	Tachinid sp.18	0	0	0	0
	Tachinid sp.19	0	0	1	1
	Tachinid sp.20	0	1	0	1
	Tachinid sp.21	0	1	0	1
	Tachinid sp.22	2	0	0	2
	Tachinid sp.23	1	0	0	1

Tachinid sp.24	0	1	0	1
Tachinid sp.25	0	2	0	2
Total Schizophora	1767	1739	2365	5871

CHAPTER 3: GENERAL CONCLUSION

This study has contributed to the knowledge of diversity patterns in Schizophora in temperate deciduous forest of three Monteregian Hills. These hills are important from a conservation perspective because they are forest fragments surrounded by agricultural fields and cities. As such, they are reservoirs of biodiversity for this region. Despite their conservation status and high diversity, there has been little study of arthropod ecological patterns in these sites.

This study builds upon some previous faunal inventories of Diptera in the Monteregian region to address more specific ecological questions about the structure of the Diptera community. This was the first study to assess forest Diptera diversity patterns across scales, although similar studies have been conducted on other forest arthropods (i.e. beetles, moths, spiders and mites). This project provides baseline knowledge for future studies of forest Diptera ecology, by presenting an optimal scale for diversity, but also by presenting potential factors influencing the species assemblage.

The results have shown that the dipteran assemblage was not random for all scales selected, and was structured at smaller scales, explaining the importance of even small differences in latitude and longitude as environmental variables. The scale contributing the most to richness was between the trees (β_1), which could correspond to an optimal scale for further studies in similar habitats. The patterns detected seem to come from a fine balance between several factors, providing some insight into ecological processes underlying the patterns. Diversity within trees (α_1) seems to be influenced by aggregation, which might result from behaviour, patchy resources, sampling effects or even local extinction rates. On the other hand, diversity between trees, stands and sites seems to come from an equilibrium between dispersal, coexistence, habitat heterogeneity and resource specialization, while niche size and trophic guild could also be important factors. These different factors are scale dependent, meaning that their impact and

importance do change across scales. An example is dispersal limitation, which should be higher at the site level than at the tree level.

Patterns did differ among groups and taxa. Assemblages of most forest arthropods studied to date were structured at broader scales; this was not the case with Diptera. It is informative not only to examine multiple spatial scales, but different subordinate groupings within the taxa studied. In this study, common and rare species did have very different patterns than the regional pool. Although, their patterns seem more consistent across different groups of arthropods studied (e.g. canopy beetles). Common species were more structured at finer scales (α_1), while rare species were more influenced by broader scales (β_3).

Future work on Diptera should consider the trophic guild as a subordinate grouping for separate analysis, in order to compare generalists to specialists, as well as species such as host-specific phytophagous Diptera that might be more directly linked to environmental factors. Specific measurements of the importance of different factors influencing species composition may also be informative. For example, the effect of habitat heterogeneity on dispersal could be tested in order to see to what extent the diversity pattern will change. More ecological study will be needed at smaller scales to determine the environmental factors explaining dipteran distribution and assemblages, to eventually identify the processes underlying them. Lastly, it would be interesting to verify the turnover rate of these assemblages in time throughout the season, as well as from year to year.