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Diversity and community structure of mosquitoes (Diptera: Culicidae) in suburban, field, and forest habitats in Montréal, Québec, Canada

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Abstract

Understanding the medical and economic impacts of mosquitoes (Diptera: Culicidae) begins with knowing their natural history and distribution, including their association with habitat types, particularly those in which human activity is high. The effects of habitat on shaping the community structure of mosquitoes were studied across periurban habitats on the island of Montréal, Québec, Canada in 2014 and 2015. Mosquitoes were collected from 20 fixed sampling locations in suburban backyards, fields, and forests, using CO₂-baited light-emitting diode encephalitis vector survey traps. A total of 184 607 mosquitoes were collected, representing eight genera and 35 species. Suburban, field, and forest sites had different communities of mosquitoes, but differences were not apparent among sites within similar habitat types in nonmetric multidimensional scaling ordinations and permutational multivariate analysis of variance. In both years, the greatest abundance of mosquitoes was collected from field habitat, and the highest species richness, from forests. Suburban sites consistently generated the lowest abundance and diversity. Nearly 75% of the total individuals collected were from three species: *Aedes vexans* (Meigen), 39%; *Coquillettidia perturbans* (Walker), 18%; and *Aedes canadensis* (Theobald), 16%. This research shows that diverse communities of mosquitoes can be found in forests, fields, and backyards, yet the communities between forests differ from more open habitats. Our community analysis reveals that medically important species (e.g., *Culex* sp.) are more commonly encountered in suburban backyards, yet overall mosquito nuisance potential is greater in forest and field habitats. This information highlights important patterns of mosquito abundance and species occurrence, vital for the development of management programmes.

Introduction

Mosquitoes (Diptera: Culicidae) are medically, economically, and ecologically important flies that live in most terrestrial habitats. In addition to being nuisance pests (Dickinson and Paskewitz 2012; Halasa *et al.* 2014) and vectors of disease-causing organisms (Gubler 1998; Norris 2004; Rochlin *et al.* 2013), mosquitoes may act as environmental indicators (Hoekman *et al.* 2016), they contribute to essential ecosystem services such as pollination (Singer 2001; Döetterl *et al.* 2012), and they are prey for highly valued vertebrates (Rueda 2008; Gonsalves *et al.* 2013). Although considerable effort has been undertaken to identify and document the range and biology of mosquito species across North America (Haddow *et al.* 2009; Buckner *et al.* 2011; Ganser and Wisely 2013), the distribution and habitat preferences of most species are not entirely understood.

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Many species of mosquitoes, including those that pose serious health risks, can be found over a wide range of habitat types (Pecoraro *et al.* 2007; Abella-Medrano *et al.* 2015; Medlock and Vaux 2015). Across a habitat gradient, populations of different species can overlap, leading to a community continuum of shared species and similarity in community structure (Whittaker 1972). Mosquito communities are not distributed uniformly in a given landscape, either temporally or spatially, in part because of environmental conditions, habitat variability, ability to disperse, and host-seeking behaviour (Zhong *et al.* 2003; Kilpatrick *et al.* 2006; Sérandour *et al.* 2010). In recent years, due in particular to a rise in the number of arbovirus epidemics and the spread of competent vector species around the globe (Juliano and Lounibos 2005; Benelli and Mehlhorn 2016; Fauci and Morens 2016), much research exists into the factors driving these events (Stoddard *et al.* 2009; Roche *et al.* 2015; Ferraguti *et al.* 2016). Knowledge of mosquito communities and how they relate to habitat type, particularly in areas where humans are present, is important for understanding the risk of disease transmission. Such understanding helps to identify habitat use by species implicated as important biting pests or disease vectors (Chaves *et al.* 2010; Johnson *et al.* 2012; Guedes and Navarro-Silva 2014; Reiskind *et al.* 2017; Burkett-Cadena and Vittor 2018) and allows streamlining of mosquito control measures at narrow landscape scales. Halasa *et al.* (2014) found that nuisance behaviour of biting mosquitoes limited the amount of time people spend outdoors, engaging in recreational activities, or simply enjoying their yards.

Our research focussed on the West Island of Montréal, Québec, Canada – a matrix of habitats that includes urban, periurban, agricultural, and green spaces (parks, forests) – and home to nearly 250 000 people (Statistics Canada 2017). The region by the island's western tip is especially important because it includes large forested areas and, therefore, is of ongoing interest and concern regarding mosquitoes and their associated diseases (Richardson 2016).

The first objective of our research was to quantify how dominant habitats – forests, fields, and suburban backyards – in Montréal's West Island affect the community structure of mosquitoes. Our second objective was to assess within-habitat differences in species-specific patterns of abundance of the most dominant and medically important species.

Methods

Study sites

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

Twenty sampling locations were chosen across different habitat types (Fig. 1). Habitat types comprised three broad categories, which were defined as “suburban” – characterised by single-family housing with parks, sparsely planted trees, and adjacent green spaces; “forest” – comprising large overstorey trees with mostly closed canopy; and “fields” – open areas lacking tree cover and composed mostly of low-growing herbaceous vegetation or agricultural crops with substantially more direct solar radiation. At least three replicate locations were sampled for each habitat type. Three locations were sampled in each of two suburban municipalities: Baie d'Urfé and Sainte-Anne-de-Bellevue. Forested habitats were located within the Morgan Arboretum, a 245-hectare forested property located within the town of Sainte-Anne-de-Bellevue. Three forest types were distinguished by dominant overstorey tree-species composition: sugar maple, *Acer saccharum* Marshall (Sapindaceae); American beech–red maple, *Fagus grandifolia* Ehrhart (Fagaceae)–*Acer rubrum* Linnaeus (Sapindaceae); and eastern hemlock, *Tsuga canadensis* (Linnaeus) Carrière (Pinaceae). Each forest type was sampled at three locations, with the exception of the sugar maple forest type, where four locations were sampled. Four field locations were sampled.

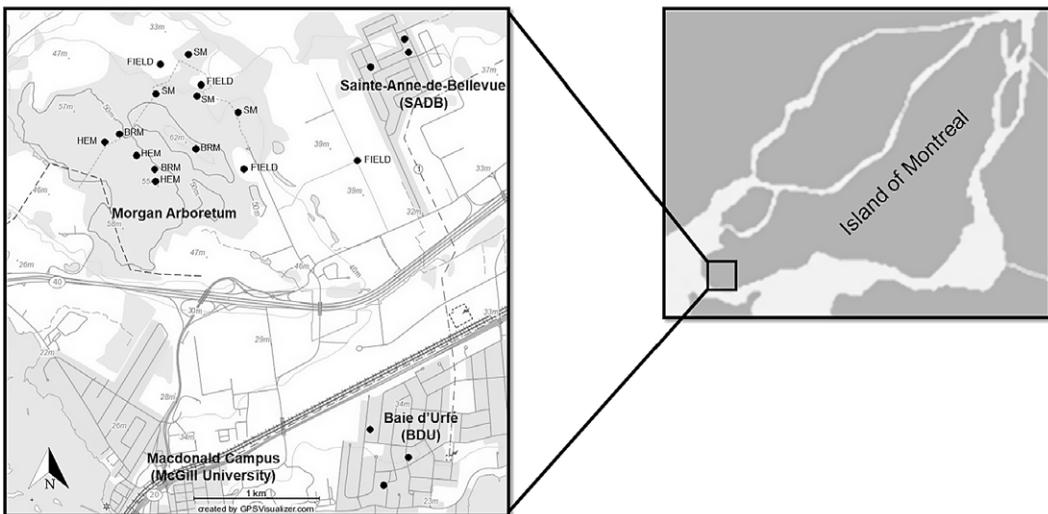


Fig. 1. Map of the study area located on the western tip of the island of Montréal, Québec, Canada. Insert shows sampling locations as black dots. Suburban locations – BDU, Baie d'Urfé; SADB, Sainte-Anne-de-Bellevue; forest types – SM, sugar maple; BRM, beech–red maple; HEM, eastern hemlock; and field.

Possible source breeding sites for mosquitoes in forested habitats included ephemeral pools, which are abundant and widely distributed in the early season but are effectively dry by mid- to late-summer. A single pond located within the Morgan Arboretum and a small, densely vegetated marsh located next to it comprise the majority of the permanent wetland habitats in the immediate area. Discarded tires, bird baths, backyard ponds, municipal rainwater ditches, and clogged gutters were some of the potential breeding sites identified within the sampled suburban areas.

The forest and field habitats are all located on conservation land, with the exception of a single field replicate located in an agricultural field. To our knowledge, none of these areas have been subjected to mosquito control measures. Within the suburban communities, control measures may have been used in the surrounding area, but they were not used on the properties of the land owners involved in the present study.

Sample collection and specimen processing. Mosquitoes were sampled in each location using all-weather light-emitting diode encephalitis vector survey traps (Bioquip Products, Inc., Rancho Dominguez, California, United States of America) that were baited with 1.5 kg of dry ice and suspended 1.5 m above the ground. Samples were taken weekly from 25 June to 1 October 2014 and from 19 April to 14 October 2015, for a total of 15 and 25 sampling weeks per year, respectively. Traps were serviced once a week for a total of 300 and 500 trap collections for 2014 and 2015, respectively. Traps were deployed in early afternoon and remained open for 24 hours to sample in all activity periods (*i.e.*, daylight, twilight, night). After 24 hours, trap bags were removed, and specimens were placed in a freezer for later identification.

Identification was done using keys to morphological characters (Wood *et al.* 1979; Darsie and Ward 2005; Thielman and Hunter 2007). All adult female specimens in the samples from each collected trap were identified to species and counted. If a specimen was too damaged to identify to species, it was counted as unknown and discarded. Damage to specimens included physical damage by the collection fan, predation within collection bags, and issues related to freezing and condensation, all of which remove essential features necessary for identification.

The naming and abbreviations used herein for all genera follow the classification outlined by Wilkerson *et al.* (2015). Voucher specimens of all species are deposited at the Lyman Entomological Museum, McGill University, Sainte-Anne-de-Bellevue, Québec, Canada.

Data analyses. Sample data from each location were pooled by year, and the locations were assigned to their respective habitat type for analysis. Analysis of variance tests was performed to identify the effect of the different locations on abundance (log +1 transformed) and species richness (total observed species). Analysis of variance was followed by the Tukey honest significant difference test for pairwise comparisons. Tests were performed using the functions `aov` and `TukeyHSD` in R, version 3.1.3 (R Core Team 2015). In all analyses, $P < 0.05$ is considered to be significant.

Habitats were further compared by analysing the mean abundance, total, unique, and shared species for each of the three broad habitat types. Mean abundance was calculated by dividing the total number of mosquitoes collected in each habitat type by the number of replicate sampling sites within each. Species accounts are based on presence–absence observations; singleton species were considered in this comparison. Shared species were used to highlight similarities between the three habitat types with respect to their overall richness.

Mean abundance (mean number of individuals per trap) and species richness (total number of species) were also calculated for each site, providing a more detailed look at the different areas sampled. Mean number of mosquitoes per site was calculated by dividing the total number of mosquitoes collected at each site by the number of trap collections. This was done to remove the effect of unequal number of trap replicates at different sites, because the inequality in sampling effort makes comparisons of species richness at different spatial or temporal scales difficult. Therefore, individual-based rarefaction estimates were generated to standardise the richness values to a sample size that is comparable across all sampling units (Buddle *et al.* 2005). Rarefaction estimates for each site were produced using the `rarefy` function in `vegan` library, version 2.2-1 (Oksanen 2015) in R, version 3.1.3 (R Core Team 2015) to generate extrapolated values beyond the observed species richness at each site. To compare species richness across the two seasons, rarefaction analysis was run on a truncated version of the 2015 data, which was generated by removing all weeks that were not sampled in both years.

Patterns of species dominance were generated by comparing rank abundance in each year and at each site by selecting the five most abundant species encountered based on total abundance. Dominant species generally made up more than 5% of the total catch in a given year (Rydzanicz and Lonc 2003, adapted from Trojan 1992), and the five highest ranked species (Burkett-Cadena *et al.* 2008; Lysyk 2010) and the medically important *Culex pipiens* (Linnaeus) (Ciota 2017; Romi *et al.* 2018) were selected. Relative proportions were calculated in regard to these species alone.

To test the effect of habitat on shaping mosquito community structure, nonmetric multidimensional scaling ordinations were generated using the function `metaMDS` in `vegan` library, version 2.2-1 (Oksanen 2015) in R, version 3.1.3 (R Core Team 2015). Detailed discussion of this method and its application in the analysis of ecological communities can be found in several works (Clark 2005; Holland 2008; Rossi 2010). Mosquito data were pooled by habitat type and area (*e.g.*, Baie d'Urfé, field, sugar maple, etc.) and by year. All data were square-root transformed to reduce the effect of very abundant species. To aid in interpretation, the `ordiellipse` function was used to superimpose the standard error as an indication of significance between sites. The significance of the interaction between habitat types was determined using a permutational multivariate analysis of variance using distance matrices, followed by the Bonferroni multiple comparison test to perform a pairwise comparison across all habitats for each year.

Results

A total of 184 607 mosquitoes were collected in the two study years: 43 443 specimens in 2014 and 141 164 in 2015. These represented 35 species (29 in 2014; 34 in 2015) in eight genera (Table 1). The genus *Aedes* had the most species (21): three species – *Aedes vexans* (Meigen) (39%), *Coquillettidia perturbans* (Walker) (18%), and *Aedes canadensis* (Theobald) (16%) – comprised nearly 75% of the total number of mosquitoes collected across both sampling seasons (Table 1).

At the time of collection, one species was thought to be newly detected in the province of Québec. This species, *Psorophora ferox* (Humboldt) (Wood *et al.* 1979; Darsie and Ward 2005), was observed as 32 individuals in 2014, increasing to 652 in 2015, with several males also collected.

Table 1. Mosquito species and total numbers collected in 2014 and 2015 from Montréal, Québec, Canada.

Species	Year	
	2014	2015
<i>Aedes</i>		
<i>abseratus</i> (Felt and Young)	0	4
<i>canadensis</i> (Theobald)	15 738	14 400
<i>cinereus</i> (Meigen)	1103	2583
<i>communis</i> (De Geer)	4	897
<i>diantaeus</i> (Howard, Dyar, and Knab)	268	423
<i>dorsalis</i> (Meigen)	2	44
<i>eudes</i> (Howard, Dyar, and Knab)	6	194
<i>excrucians</i> (Walker)	727	538
<i>fitchii</i> (Felt and Young)	274	528
<i>implicatus</i> (Vockeroth)	0	17
<i>intrudens</i> (Dyar)	0	48
<i>japonicus</i> (Theobald)	18	40
<i>pionips</i> (Dyar)	6	42
<i>provocans</i> (Walker)	41	6533
<i>punctor</i> (Kirby)	13	2075
<i>rempeli</i> (Vockeroth)	0	5
<i>sticticus</i> (Meigen)	9	24
<i>stimulans</i> (Walker)	2317	6,003
<i>triseriatus</i> (Say)	366	330
<i>trivittatus</i> (Coquillett)	1289	15 646
<i>vexans</i> (Meigen)	10 569	62 169
<i>Anopheles</i>		
<i>earlei</i> (Vargas)	0	1
<i>punctipennis</i> (Say)	92	304
<i>quadrimaculatus</i> (Say)	4	8
<i>walkeri</i> (Theobald)	85	188

(Continued)

Table 1. (Continued)

Species	Year	
	2014	2015
<i>Coquilletidia</i>		
<i>perturbans</i> (Walker)	8897	24 588
<i>Culex</i>		
<i>pipiens</i> (Linnaeus)	315	1,169
<i>restuans</i> (Theobald)	9	21
<i>Culiseta</i>		
<i>melanura</i> (Coquillett)	1	19
<i>minnesotae</i> (Barr)	0	42
<i>morsitans</i> (Theobald)	67	93
<i>Orthopodomyia</i>		
<i>alba</i> (Baker)	1	0
<i>Psorophora</i>		
<i>ciliata</i> (Fabricius)	1	61
<i>ferox</i> (Humboldt)	32	652
<i>Uranotaenia</i>		
<i>sapphirina</i> (Osten Sacken)	269	989
Unidentifiable	920	486
Total no. of individuals	43 443	141 164

Community structure

Community structure was distinct across the habitat types for both years (Fig. 2). The mosquito communities showed clear separation between the habitat types in the ordination space. The lack of overlap between the observed means suggests dissimilarity. Permutational multivariate analysis of variance results using Bonferroni multiple comparison tests on pairwise habitat groups showed that all habitats were significantly different, with the exception of suburban compared to field habitats in 2015 (Table 2). Within the habitat types, the sites showed little variation as seen by the overlap in sample means (Fig. 2); this was especially evident when comparing forest and suburban sites.

Table 2. Permutational multivariate analysis of variance post-hoc analyses habitat comparisons for 2014 and 2015.

Between-habitat interaction	Adjusted <i>P</i> -values
2014	
Suburb <i>versus</i> field	0.015
Suburb <i>versus</i> forest	0.030
Field <i>versus</i> forest	0.030
2015	
Suburb <i>versus</i> field	0.075
Suburb <i>versus</i> forest	0.015
Field <i>versus</i> forest	0.015

Significant *P*-values are indicated in bold.

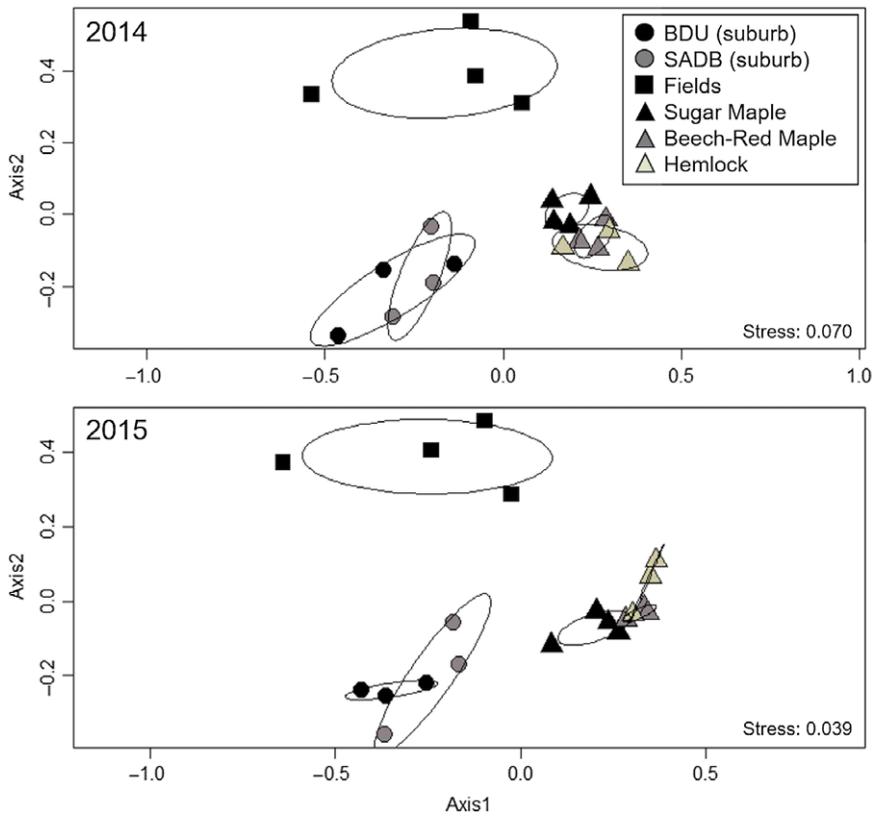


Fig. 2. Nonmetric multidimensional scaling ordinations for both 2014 (top) and 2015 (bottom). Ellipses represent the standard error about the mean for each site. Stress values: 2014 (0.070); 2015 (0.039).

Abundance and species richness

Mean abundance and species richness at the level of habitat varied between habitat types, and patterns were maintained between years (Fig. 3). Suburban habitat consistently had the lowest mean abundance and species richness. Field habitat maintained the highest mean abundance in both years, and forests had the highest species richness.

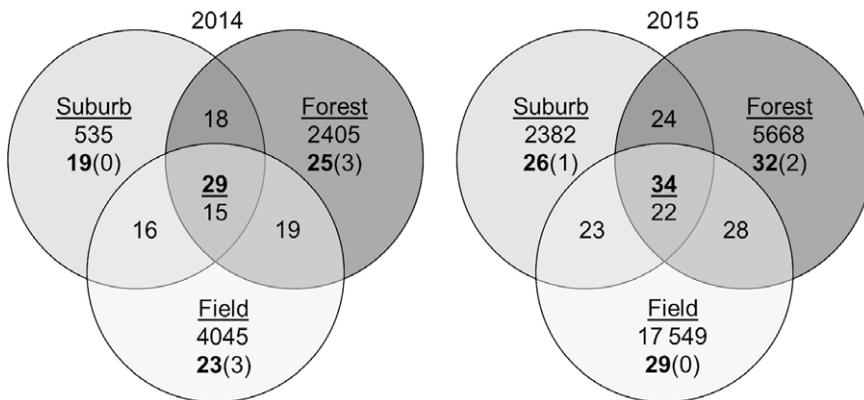


Fig. 3. Mean abundance (per replicate), species richness, and shared species for each habitat type for 2014 and 2015. Mean number of mosquitoes per replicate appears first, numbers in bold indicate total number of species collected, and numbers in parentheses show the number of unique species. Numbers in overlapping areas indicate the number of shared species. Total species collected (bold and underlined), as well as the total number of shared species for each year, appear in the centre of each diagram.

Across both sampling seasons, the mean abundances per trap were highest in field habitat and lowest in suburban areas (Fig. 4). Similar to habitat comparisons, species richness per site increased along a gradient of decreasing disturbance, with the lowest values in suburban areas, slightly higher values occurring in fields, and the highest values found in forested sites (Fig. 5). This pattern was consistent in both years. Among the forest types, eastern hemlock forests maintained the highest abundance and diversity in both years (Figs. 4 and 5). Rarefied species richness shows that the expected number of species was highest in Baie d'Urfé in 2014 and highest in eastern hemlock forest sites in 2015 for both the full data set and the truncated subset, which mirrors the same sampling period in 2014 (Supplementary material, Appendix 1). All rarefied estimates based on the lowest number of individuals collected at a given site in each year were lower than the actual number of species collected at each site, suggesting that overall, sites were sampled adequately. The municipality of Baie d'Urfé contained the lowest number of individuals collected in all three generated rarefaction estimates and was used as the basis for comparison. Interannual patterns of abundance can further be analysed with the inclusion of environmental data, particularly rainfall and temperature (Supplementary material, Appendix 2).

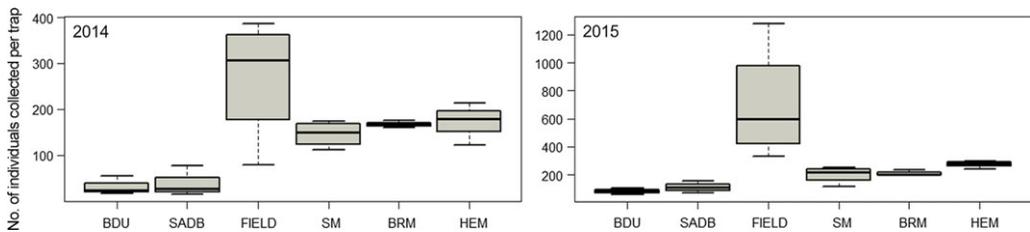


Fig. 4. Mean number of individuals collected per trap for all six sites in 2014 (left) and 2015 (right). Boxes show the upper and lower quartiles, the horizontal line within the box shows the median value, and the whiskers show the maximum and minimum observed values.

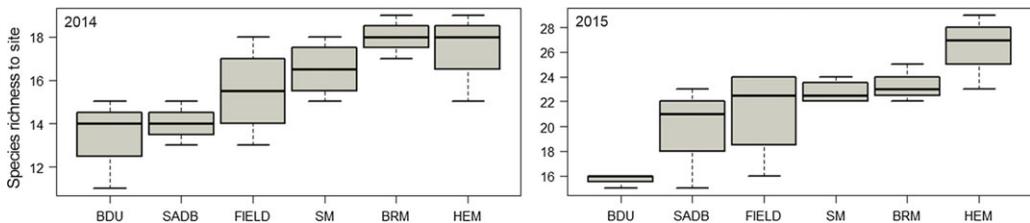


Fig. 5. Species richness for all six sites in 2014 (left) and 2015 (right). Boxes show the upper and lower quartiles, the horizontal line within the box shows the median value, and the whiskers show the maximum and minimum observed values.

When tested using an analysis of variance, the “site” factor was significant for abundance and richness in both years. When tested individually using pairwise comparisons (Tukey honest significant difference test) between sites, the significance of abundance and species richness varied; Baie d'Urfé–Sainte-Anne-de-Bellevue interactions and the interactions between all forested sites were not significant. These results support the patterns observed with ordination, in that multiple sites within a similar habitat do not generate any significant differences in abundance or observed richness with pairwise comparisons (Table 3).

Table 3. Analysis of variance results for abundance and richness across all sites for 2014 and 2015.

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

Significant *P*-values are shown in bold.

BDU, Baie d'Urfé; BRM, beech-red maple; FIELD, fields; HEM, eastern hemlock; SADB, Sainte-Anne-de-Bellevue; SM, sugar maple.

Shared species

Nearly 52% of all species encountered were shared between the three habitat types in 2014; almost 65% of species were shared in 2015. The number of shared species in both years was highest between forest and field habitat and lowest between field and suburban habitat (Fig. 3). Suburban habitat in general shared a greater number of species with forests than with fields. Forest habitats had the highest number of unique species in each year: three in 2014 (equal to fields) and two in 2015.

Species-specific patterns

Relative abundance of dominant species differed between habitats in both years (Fig. 6). All dominant species occurred in every site; however, some were present in such low numbers that their relative proportion represented less than 1% and did not contribute greatly to this dominance matrix.

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

In 2015, suburban sites were again dominated by *Ae. vexans* but to an even greater degree than in 2014. Field habitat was again co-dominated by *Ae. vexans* and *Cq. perturbans* but with the former having higher relative abundance. Forested sites remained the most suitable habitat for *Ae. canadensis* but with lower relative abundance than in 2014. Relative abundance of

Ae. trivittatus was much higher in forested sites compared to the 2014 results. A clear preference for forested sites was seen in *Ae. provocans* (Walker), with greater representation in American beech–red maple and eastern hemlock forest sites than in the sugar maple forest areas.

One species, *Cx. pipiens*, showed strong association with the more disturbed areas, being found in greatest total numbers in suburban sites, with fields being the next most preferred sites. This species' occurrence in forested habitats was almost negligible; the eastern hemlock forest sites generated the greatest total catches with five individuals in 2014 and 37 in 2015.

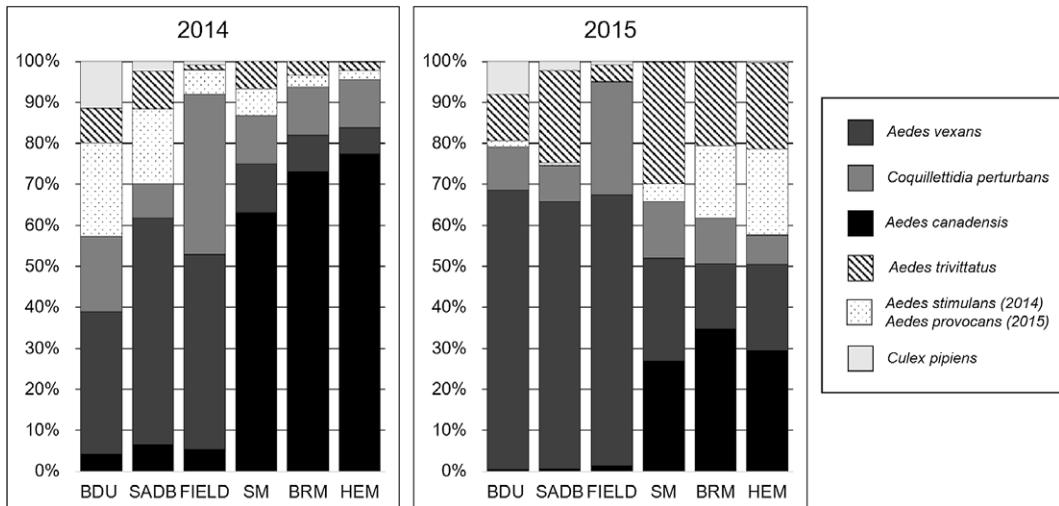


Fig. 6. Relative abundance of the five most abundant species collected from each of the six sites in both 2014 (left) and 2015 (right). Note: Four of these species were ranked highest in both years, and the fifth position was held by different species in 2014 and 2015 – these being *Aedes stimulans* and *Aedes provocans*, respectively. *Culex pipiens* is included due to its West Nile virus vector potential.

Discussion

Mosquitoes are abundant and widely distributed around the world, with unparalleled medical and economic importance as pests and vectors of disease (Ramasamy and Surendran 2016; Wilder-Smith *et al.* 2017), and yet the structure of mosquito communities by habitat type has been poorly studied, especially in Canada. Our research compared mosquito communities among three dominant habitats on the island of Montréal, Québec, with the goal of identifying how mosquito communities are structured in relation to habitat type and how mosquito abundance, richness, species sharing, and species dominance varied between the sites. We determined that mosquito communities are distinct when compared across habitat types that are markedly different – in this case, between suburban areas, fields, and forested sites. Community structure varied little when comparisons of like-habitats were performed – for example, between multiple forest stands or between different suburban neighbourhoods. Values for mean abundance were always highest in field habitat, and species richness was greatest in forests. Suburban areas were the lowest in both categories. The dominant species remained essentially the same in both sampling years, and each habitat had its own complement of dominant species. Medically important species such as *Cx. pipiens* were found in greatest number in suburban habitat. Our extensive sample collection revealed the presence of a little-known species for the province of Québec, *Psorophora ferox* (Humboldt). Further investigation uncovered very few records of this species occurrence in the province (Lowe *et al.* 2017), and our findings may indicate this species' range expansion. Field, suburban, and forested habitats support distinct assemblages of

mosquitoes (Table 2; Fig. 2). Within-habitat differences were less pronounced, suggesting that like-habitats support similar communities. This result is consistent with the literature; other studies suggest that habitat ultimately is the main driver in determining community structure, although between-habitat similarities can exist (Zhong *et al.* 2003; Yan and Zhong 2005).

Recent studies examining the effect of disturbance gradients revealed that communities vary with habitat type, and that abundance and species richness tend to increase along the gradient from disturbed anthropogenic habitats to more pristine environments (Rochlin *et al.* 2008; Stein *et al.* 2016; Reiskind *et al.* 2017). Site is a significant factor in structuring communities, likely relating to habitat structure and the availability of breeding sites (Ganser and Wisely 2013; Alencar *et al.* 2015; Golding *et al.* 2015). Successful development of larvae is linked to the availability of breeding sites and also to habitat-driven qualities, including water quality, light intensity, organic inputs, temperature, and biotic interactions – factors that vary among habitats (Becker *et al.* 2003; Kling *et al.* 2007; Juliano 2009; Fader and Juliano 2014; Hunt *et al.* 2017). Our study demonstrates an increase in species richness along a habitat gradient from suburban to forest habitats (Figs. 3 and 5). Reasons for this could include the increased structural complexity in forests, which increases breeding opportunities and provides a greater density of hosts (Tews *et al.* 2004; McElhinny *et al.* 2005; Johnson *et al.* 2012). Stein *et al.* (2016) found that semiurban and pristine wild areas contained the greatest richness of species, compared to more human-altered environments. Zhong *et al.* (2003) and Johnson *et al.* (2008) also found that complex habitats offer a greater variety of landscape features with increased structure. Poppe *et al.* (2015) argue that forests also offer greater stability than other, more disturbed sites. In the present study, field habitat showed greater diversity than suburban sites did, possibly due to its proximity to forested habitats relative to suburban areas (Fig. 1). Although the suburban areas were more favourable for container-breeding species like *Cx. pipiens* and the invasive rock pool mosquito *Aedes japonicus* (Theobald), these species were also detected in low numbers in other habitats. Conversely, a greater number of species occurred in forested areas that were not detected in suburban yards. Rarefaction estimates of species richness suggest that all sites were adequately sampled, and truncating values for 2015 to mirror the same sampling period for 2014 did not alter the trends of species richness of the rarefied estimates (Supplementary material, Appendix 1). Although our analysis shows that the habitats were adequately sampled, it is possible that more species could have been detected had we incorporated different collection methods. Light traps, especially those augmented with CO₂, are traditionally the best for maximum diversity; however, sampling larvae or sampling adults at different stages of their reproductive cycle may have yielded additional species (Hoekman *et al.* 2016). Additionally, because some species are restricted in their habitat requirements, inclusion of a greater diversity of habitats or increased daytime sampling could improve the chances of encountering additional species (Crans 2004; Heokman *et al.* 2016).

The observed patterns in mean abundance and species richness at the habitat level suggest that these parameters are maintained from year to year (Fig. 3). However, seasonal fluctuation in mosquito communities can occur, likely because of environmental conditions such as temperature and rainfall, which fluctuate annually (Lysyk 2010; Buckner *et al.* 2011; Ganser and Wisely 2013). Long-term studies are needed over multiple years to generate average values of abundance and species richness.

We quantified adult mosquito abundance by evaluating the mean number of adults collected in each of the three broad habitat types (Fig. 3) and also per trap to compare these values across all six sites (Fig. 4). Trap collections were highest in open field habitats. This finding is consistent with the work of Steiger *et al.* (2012), who collected a greater abundance of mosquitoes in grassland habitat, compared to forest interior and edge habitat. Females disperse in response to stimuli like traps or hosts (Bidleimayer and Hem 1981), and light traps in open areas are more visible. The ability of individual species to locate traps and disperse from source areas would influence apparent species distributions and abundance (Schowalter 2011). Field captures in the present study comprised mainly *Ae. vexans* and *Cq. perturbans* – species known to travel long distances

in search of suitable hosts (Cupp *et al.* 2003; Turell *et al.* 2005; Abella-Medrano *et al.* 2015). Short- to long-range wind dispersal allows mosquitoes to locate hosts and breeding sites (Service 1980; Cummins *et al.* 2012), except for container-breeding species, which may have a more limited dispersal distance (Bellini *et al.* 2010). We recognise that sampling across distinct habitat types creates a situation in which the habitat itself may alter the capture rates of mosquitoes. This may lead to overestimation or underestimation of abundance depending on the habitat type. Within suburban habitat, competing light sources (porch lights, street lights, *etc.*; Barghini and de Medeiros 2010) and different sources of CO₂ (vehicles, people, *etc.*) may result in dilution of mosquitoes attracted to baited light traps.

Studies of community ecology often rely on spatial occurrence of species in simple presence–absence matrices to draw conclusions about community dynamics (MacKenzie *et al.* 2004). Here, we compare the distribution of species across different habitat types and reveal patterns of species co-occurrence, unique species, and mean abundance (Fig. 3). Several of the species found in each habitat type were represented in low numbers, which may indicate incidental captures outside their typical habitat preferences. Steiger *et al.* (2012) found that half of their species occurred in all habitat types, with few habitat specialists – a finding similar to ours (Figs. 3 and 6). Similarly, Abella-Medrano *et al.* (2015) noted a high degree of species sharing between sites with different land-uses, and similarly again to this study, they found that abundance was highly variable, suggesting that resource availability varies across space and time, thereby shaping distribution. Contrary to our findings, Reiskind *et al.* (2017) noted that more than half the species encountered in their study were clearly faithful to one habitat type or another across a field-to-forest gradient. Close proximity of the sampling locations in the present study likely resulted in a higher degree of species sharing. Despite the structural differences experienced in each of the habitat types, the attractiveness of CO₂-baited light traps likely drew species from greater distances and from a diversity of surrounding habitats (Bidlingmayer and Hem 1981).

The degree of species sharing showed similar trends across both years (Fig. 3). Forest and field habitats consistently had the highest number of shared species, whereas suburbs and fields had the lowest. Interestingly, suburban yards shared the greatest number of species with forested habitats, despite suburban sites having the lowest number of recorded species and forested sites having the highest number. This may indicate the importance of vertical structure in determining habitat preference, as both these habitats contain trees. Trees offer a variety of breeding opportunities in the form of tree holes, a particular habitat known to be used by many species (Wood *et al.* 1979; Bradshaw and Holzapfel 1992; Srivastava and Lawton 1998). Gardner *et al.* (2017) demonstrated that the presence of a single plant species was enough to have a substantial impact on mosquito abundance and survival and also disease transmission. These findings emphasise the importance of mosquito–plant interactions and a need for understanding these at multiple scales. Several additional species were recorded in the suburban sites in 2015, especially at Sainte-Anne-de-Bellevue, which saw a marked increase from 18 species in 2014 to 26 in 2015 (Fig. 3).

Species-specific patterns

Within a community, some species would be considered very common (dominants) and others moderately abundant or rare (Whittaker 1965). Dominant species are important to consider because they contribute greatly to shaping community structure and they reveal patterns of nuisance and vector potential (Meide *et al.* 2008; Guedes and Navarro-Silva 2014). In the present study, similar species dominated the total catch in both sampling years, and our findings reveal that species dominance depends on habitat type (Fig. 6). Four species clearly had the highest abundance and, thus, greatest dominance: *Ae. vexans*, *Cq. perturbans*, *Ae. canadensis*, and *Ae. trivittatus* (Table 1; Fig. 6). Patterns of dominance were maintained between like-habitats (Fig. 6). Abella-Medrano *et al.* (2015) also found that dominance was always attributed to four species, regardless of site – a pattern similar to the one we found.

All species considered dominant in the present study were encountered in all sites, but their relative proportion varied. Within suburban sites, *Ae. vexans* contributed the greatest number of individuals. This species breeds in a variety of habitats, and numbers swell following periodic rain events (Wood *et al.* 1979; Crans 2004). Suburban sites also produced large numbers of *Ae. stimulans* in 2014 and of *Ae. trivittatus* in 2015. Field habitat was dominated by two principal species, *Ae. vexans* and *Cq. perturbans* – both known to frequent open-area habitats (Carpenter and LaCasse 1955; Howard *et al.* 1983; Bosak *et al.* 2001). Forested sites had large numbers of *Ae. canadensis*, a species that prefers shaded woodland pools or mixed woodland habitat (Carpenter and LaCasse 1955; Wood *et al.* 1979; Nasci *et al.* 2000). The relative abundance of this species was lower in 2015, likely because of the extended sampling season in 2015, during which we collected higher numbers of *Ae. trivittatus* and *Ae. provocans*, two species that generally emerge earlier in the season than *Ae. canadensis* does (Wood *et al.* 1979) and therefore may have been missed in 2014. A noted difference is the replacement of *Ae. stimulans* in 2014 with *Ae. provocans* in 2015 amongst the dominant species. Again, this likely is related to the earlier start to sampling in 2015, which would have produced larger numbers of *Ae. provocans*. To best represent the relative abundance and dominance hierarchy, sampling should begin at the earliest date possible. Temporal variation in dominance can also be analysed by looking at samples over defined time periods instead of collectively for a year.

Because of its medical importance in the transmission of West Nile virus (Andreadis *et al.* 2001; Turell *et al.* 2005), the distribution of *Cx. pipiens* across habitat types is integral to our understanding of local vector ecology. The comparison of species dominance by site (Fig. 6) shows that this species occurs mainly in suburban sites, a finding that is common in the literature (Kling *et al.* 2007; Pecoraro *et al.* 2007; Junglen *et al.* 2009; Johnson *et al.* 2012). This species is known to use artificial breeding sites associated with peridomestic water sources (Norris 2004; Yee 2008; Deichmeister and Telang 2011). No other dominant species collected, particularly in suburban habitats, use containers to the extent that *Culex* does; thus, competition in these habitats is minimal (Wood *et al.* 1979; Crans 2004). Our findings suggest that suburban areas are likely an important source of *Culex* mosquitoes and that programmes to combat West Nile virus should focus on these areas. Other species encountered during this study, including the five most abundant species, have also been shown to be carriers of West Nile virus but with varied vector competence (Turell *et al.* 2005; Centers for Disease Control and Prevention 2012). Province-wide mosquito surveillance and collection of arbovirus infection data are handled by the Ministère de la Santé et des Services Sociaux du Québec. On the island of Montréal, pools of mosquitoes are tested weekly from five sampling stations. Sampling has been conducted annually since 2003. As of 2016, inclusion of Eastern equine encephalitis and California serogroup virus surveillance has been integrated into the existing West Nile virus surveillance programme (Institut national de santé publique du Québec 2017). Competent vector species – for example *Culex* sp. (West Nile virus), *Culiseta melanura* (Eastern equine encephalitis), and a variety of other, non-*Culex* mosquitoes (California serogroup virus) – are the main focus of such investigations. Invasive species, particularly *Aedes* spp. recently detected in Canada, are also under surveillance (Institut national de santé publique du Québec 2017; Ludwig *et al.* 2019).

Conclusions

This study provides information about the community structure, distribution, abundance, and interactions of mosquito species in a heterogeneous landscape in Montréal, Québec, Canada. Our findings suggest that habitat plays an important role in shaping mosquito community structure. Across the three broad habitat types, communities are distinct, and this pattern was maintained interannually. Sites with similar physical structure – for example, multiple forest types or suburban neighbourhoods – show greater similarity in their mosquito communities. Habitats that differ

structurally also vary in species dominance and mean abundance, with few exceptions. Overall, forested habitats and adjacent fields support a greater diversity of species and greater abundance of mosquitoes than suburban habitats do. More than half of all species encountered were collected in all habitat types, whereas others showed strong affinity for one habitat.

The close association between suburban habitats and *Cx. pipiens* is an important finding, in terms of West Nile virus surveillance and management in the province of Québec, elsewhere in Canada, and in the United States of America. In terms of vector-species distribution, our findings support the need for unilateral investigation into periurban habitats and a lesser need to expand surveillance into more remote environments. This potentially could help to greatly reduce the costs associated with widespread surveillance while focussing efforts where needed. With respect to disease vectors such as *Cx. pipiens*, the effect of small-scale habitat characteristics, particularly those in suburban areas, likely is important to the proliferation and vector potential of this species and requires more study. More research is also needed to examine mosquito community structure at larger spatial scales and across more habitat types. Including environmental parameters such as temperature and precipitation in future research will further improve our understanding of the spatial and temporal patterns of mosquito occurrence and seasonal phenology and how these relate to the insect's community structure.

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