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Saproxylic Diptera assemblages in a temperate deciduous forest: implications for community assembly

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Saproxylic insects, those that feed on wood or bark, compose a large proportion of forest organisms. Flies (Diptera) are often the most abundant and species-rich groups in forest microhabitats, yet most work to date on saproxylic insect diversity and ecology has focused on beetles (Coleoptera). We compared saproxylic Diptera assemblages reared from two tree species (sugar maple and American beech) at two stages of decay (ca. two years, and ca. six years after death) for a total of 20 logs in an eastern Canadian Nearctic old-growth forest. We found that communities are distinct within both species type and decay stage of wood. Early decay stage wood is more variable in community composition than later decay stage; however, as the age of the decaying wood increases, the abundance of Diptera increases significantly. Most indicator species are discernible in later decay stage and wood type. Both stochastic and deterministic processes seem to play a role in community of temperate deciduous forests. To retain the highest saproxylic Diptera diversity in a forest, a variety of decaying wood types at different stages of decomposition is necessary.
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Saproxylic insects, those that feed on wood or bark, compose a large proportion of forest organisms. Flies (Diptera) are often the most abundant and species-rich groups in forest microhabitats, yet most work to date on saproxylic insect diversity and ecology has focused on beetles (Coleoptera). We compared saproxylic Diptera assemblages reared from two tree species (sugar maple and American beech) at two stages of decay (ca. two years, and ca. six years after death) for a total of 20 logs in an eastern Canadian Nearctic old-growth forest. We found that communities are distinct within both species type and decay stage of wood. Early decay stage wood is more variable in community composition than later decay stage; however, as the age of the decaying wood increases, the abundance of Diptera increases significantly. Most indicator species are discernible in later decay stage and wood type. Both stochastic and deterministic processes seem to play a role in community of temperate deciduous forests. To retain the highest saproxylic Diptera diversity in a forest, a variety of decaying wood types at different stages of decomposition is necessary.

Keywords: dead wood, flies, community assembly, American beech, sugar maple, coarse woody debris
Introduction

Understanding the factors influencing processes of species assembly is important in community ecology research (Keddy 1992). There has been a debate in community ecology to determine whether community assembly are driven by deterministic processes, i.e. species are assembled by predictable realized niches (Hutchinson 1959), or by stochastic processes, i.e. community assemblages are randomly achieved (e.g. Hubbell 2001). There is increasing support from a wide range of study systems that both deterministic and stochastic processes are acting simultaneously (e.g. microbial communities: Caruso et al. 2011; Stegen et al. 2012; Dini-Andreote et al. 2015; arthropod communities: Thompson and Townsend 2006; Ellwood et al. 2009; Rominger et al. 2009; Fišer et al. 2012; Ferrenberg et al. 2016). However, to what extent and when these processes influence community assembly, and which organisms are affected remains to be determined for diverse taxa (Barber & Marquis 2011), including forest-dwelling and wood-inhabiting invertebrates.

A proportion of forest invertebrates are wood- or bark-inhabiting species and have a significant role in wood decomposition in temperate regions (Ulyshen 2016). The reduction of old growth forest area and implementation of forest management practices, such as clear cutting and timber harvesting, negatively impact several wood associated arthropod taxa (Buddle et al. 2006; Pohl et al. 2007; Grodsky et al. 2017). Many studies have demonstrated the importance of coarse woody debris (CWD) in maintaining forest arthropod diversity, especially of saproxylic species (fungivores, xylophages, predators, parasites, parasitoids, detritivores) associated directly or indirectly with decaying wood for all or part of their life cycle (Speight 1989; Grove 2002; Jabin et al. 2004; Lemperiere and Marage 2010; Grodsky et al. 2017). There is evidence based
on observations that tree species and, to a lesser extent, the age of the CWD have an effect on
which beetle (Coleoptera) species are present in the decaying wood (Stokland 2012).

Most work to date on saproxylic insect diversity and ecology has focused on beetles but
flies (Diptera) are often as or more abundant and species-rich in the same microhabitats (Schiegg
2000; Rotheray et al. 2001; Vanderwel et al. 2006; Persson et al. 2013). Stokland & Siitonen
(2012) stated that there are more saproxylic Diptera than Coleoptera in Nordic countries;
additionally, other studies in Europe have found that the Diptera families: Mycetophilidae,
Sciaridae and Cecidomyiidae, are particularly dominant and species-rich in decaying logs (Irmler
et al. 1996; Økland 1994; Hövemeyer & Schauermann 2003). With the exception of work by
Work & Hibbert (2011), there has been little empirical study of patterns of diversity or
microhabitat use in saproxylic Diptera in North America, particularly at taxonomic scales below
that of family.

Previous studies of saproxylic Diptera diversity in North America have been based on
course taxonomic sorting (generic or family-level identification only; e.g., Vanderwel et al. 2006;
Batzer & Braccia 2008; Dennis et al. 2017); however, coarse taxonomic sorting of Diptera may
not provide the necessary detail to study community assembly in this group. Many Diptera
families are ecologically diverse, with documented differences in microhabitat use, trophic role
and seasonal activity even within a genus (Ferrar 1987; Lévesque-Beaudin & Wheeler 2011).
Species-level identification of Diptera communities, where possible, is necessary to accurately
document fine-scale patterns of habitat use and community ecology. If conservation of
saproxylic insect fauna is to be added to forest management guidelines, a better understanding of
community patterns, with identifications done at the species-level, and responses to disturbances
is needed.
We studied saproxylic Diptera reared from decaying logs of sugar maple (Acer saccharum Marshall) and American beech (Fagus grandifolia Ehrhart) at two stages of decay (ca. two years, and ca. six years after death) in an eastern Nearctic old-growth forest. Sugar maple and American beech are the two dominant tree species in this type of forest. The objective of our study was to determine the effect of host-tree species and decay stage on community composition and community assembly of saproxylic Diptera. Based on past research focused on saproxylic Coleoptera (reviewed in Stockland 2012; Stockland & Siitonen 2012), we predicted that if Diptera communities react similarly to wood decay, they should be affected by the decay stage and tree species. We expected that there would be some species turnover between decay stages, and that community composition should be somewhat unique between tree species (Stockland & Siitonen 2012).

Material and Methods

Study site and sampling

The study was conducted at the Mont Saint-Hilaire Biosphere Reserve in Southern Quebec, Canada (45°32’40”N, 73°9’5”W) within 500m of the shore of Lac Hertel at the Reserve between 173 and 223m elevation (Suppl. Fig. 1). The Reserve is dominated by a closed canopy, old-growth, hardwood beech-sugar maple forest, which is the most common forest type in Southern Quebec.

We chose sugar maple and American beech because they are the dominant trees at the Reserve and they have similar wood hardness (Janka hardwood index: 1450 for sugar maple vs 1300 for beech), decay rates and other wood properties (Johnson et al. 2014). The main
difference between the two species is the characteristics of their bark: American beech bark has smoother bark than sugar maple.

Five fallen logs per tree species (sugar maple and American beech) and per decay stage (approximately two and six years after tree death) were selected for a total of 20 decaying logs. The decay stages were determined by visual inspection. Early decay logs were characterized by having 10–20% of the bark absent, and the first centimeters of the logs had been infiltrated by moisture and sapwood structural decay. Advanced decay logs had 80% or more of the bark absent and the heartwood had been infiltrated with moisture and decay. The logs chosen were in stands dominated by the particular species and in close proximity to other logs of the same species (i.e. the sugar maple logs were in sugar maple dominated stands in proximity of other maple sugar logs) to ensure connectivity and allow saproxylic insect colonization from the appropriate species to the logs (Schiegg 2000). All the logs had to be between 18 and 22 cm in diameter. In May 2004, the selected branchless logs were cut (1.2 m in length) on site. Once cut, each log was repositioned in its original location on a plastic ground sheet (to exclude insects emerging from soil or litter). Each log was then covered by an emergence trap (with a collecting jar at one end), which was placed on and sealed to the plastic ground sheet, to prohibit any further colonization (Irmler et al. 1996). The insects emerging from the log were collected into the collecting jar filled with a 50% solution of propylene glycol and water. These jars were collected weekly from 03 June to 16 September 2004 (16 weeks). This period corresponds to the vegetation period and the main period of insect activity.

Specimen preparation and identification

All insects were stored in 70% ethanol, then chemically dried and mounted for identification. Diptera were identified to named species where taxonomic expertise and available
literature permitted (Suppl. Table). Where identification to named species was unavailable specimens were sorted to morphospecies based on standard morphological characters (McAlpine et al. 1981) used in the literature for identification of related taxa. The specimens identified to morphospecies were numbered with a unique identifier for this study (e.g. *Sciara* sp. jm1), which are databased. These unique identifiers will allow future research (taxonomic or ecological) easy access for verification and comparison of these specimens to others in similar studies. All specimens are deposited in the Lyman Entomological Museum (McGill University, Ste-Anne-de-Bellevue, QC.).

Analyses were based on all Diptera except: Cecidomyiidae (focus of a separate study); the sciarid genera *Bradysia, Corynoptera, Lycoriella* and *Scaptosciara*, each of which was represented by multiple morphospecies that can only be distinguished after dissection and slide-mounting; and the phorid genus *Megaselia*, which was represented by several morphospecies that could not be reliably distinguished.

Each species was assigned to a trophic group based on their larval feeding habit among fungivore, saprophage, predator, parasite, omnivore and phytophage. Trophic habits were determined according to information given in Ferrar (1987) and other available literature (e.g. Pritchard 1983; Brown 1985; Brown & Hartop 2017).

**Statistical Analyses**

**Diversity patterns**

Using the pooled data for each treatment, Simpson’s reciprocal diversity index (1/D) was calculated as an evenness measure with 10 individuals for the upper abundance limit for rare species and 100 runs of randomization for estimators (Hill 1973). Extrapolated species richness was assessed using a bias-corrected Chao index (O’Hara 2005). Species diversity and sampling
efficiency was examined using individual- and sample-based rarefaction curves (Gotelli & Colwell 2001). Expected species richness of each treatment were calculated using rarefaction estimates standardised to 445 individuals which is the lowest number of individuals collected in the young maple (YM) treatment. All analyses were performed using the vegan package (Oksanen et al. 2012) in R 3.4.2 (R Development Core Team 2017).

The habitat association of each species was examined using indicator species analysis performed with the function multipatt in the package indicspecies (De Caceres & Legendre 2009). Each species was tested for its association with tree species and decay stage separately or in combinations. The significance of species association was assessed with a permutation test using 999 permutations. Only species with ≥10 individuals and an indicator value ≥45% were considered.

Generalized linear model (GLM) (McCullagh & Nelder 1989) with Poisson distribution for counts was used to evaluate the relationships between abundance, species richness, estimated species richness (Chao) and Simpson’s diversity index as response variables with decay stages and tree species as predictors. Each predictor was tested one by one, then in combination. As Margules et al. (1987) demonstrated that interactions between variables often provide a higher predictive power than the same variables separately; the interaction was tested and ranked according to Akaike Information Criterion (AIC). The model with the lowest AIC value was selected as the best model.

Community composition

Community composition among treatments was compared using non-metric multidimensional scaling (NMDS). Permutational multivariate analysis of variance based on a Bray-Curtis distance matrix was used to assess significance of differences among treatments for
overall species assemblages using the function Adonis. Prior to NMDS and Adonis, species abundances were Hellinger transformed (Legendre & Gallagher 2001), because this transformation is particularly suited to species abundance data, as it gives low weights to low counts and many zeros.

To test the spatial arrangement of species we used null model analysis with EcoSim version 7.71 (Gotelli & Entsminger 2010). This tested whether or not Diptera species collected in the different treatments are distributed in a random manner with regard to each other.

Community structure indices were computed for all logs pooled by treatment types and each tree species and decay stage separately. Co-occurrence analysis was performed using the C-score (Stone & Roberts 1990) index that measures the average number of checkerboard units (species mutual exclusion) between all possible pairs of species in a presence-absence matrix. To find a non-random pattern of species co-occurrence, the C-score should be significantly lower or higher than expected by chance. A Monte Carlo null model simulation was used to randomize the matrix 5000 times with the sequential swap algorithm and fixed sum rows and columns constraints.

Results

Diversity patterns

A total of 3034 specimens representing 227 named species and morphospecies were used in the analyses (Appendix 1). Overall the most abundant families were Milichiidae (891 specimens), Empididae (470 specimens), Limoniidae (438 specimens) and Mycetophilidae (306 specimens). The most species rich families were Mycetophilidae (50 species), Empididae (29 species), Sciaridae (20 species) and Limoniidae (19 species). Milichiidae abundance was divided between
only two species, with *Neophyllomyza quadricornis* Melander being the most abundant species overall (721 specimens; Brochu & Wheeler 2009). Trophic structure was similar in all four treatments (Fig. 1). Saprophages were the most abundant, followed by fungivores or predators and parasites being the least abundant (Fig. 1A). As for trophic richness, saprophages were the most species rich, followed by fungivores, predators and parasites (Fig. 1B). Phytophages and omnivores were excluded as they were represented by only two species each.

In the treatments, 48% of the collected species were represented by only one or two specimens. Chao indices suggested that between 83 to 88% of the species present were collected. The rarefaction curves for all treatments did not reach an asymptote (Fig. 2) and the sample-based rarefaction curves showed that none of the sampling was distinctly better, as curves for the four treatments were not significantly different (Fig. 3).

Indicator species analysis revealed that 15 species among fungivores, saprophages, predators and parasites were significantly associated with tree species, decay stage or a combination of the two (Table 1); however, there were no indicator species associated with just young decay. All indicator values were relatively low, below 75 and there was no tendency for fungivores or saprophages to have higher indicator value than any other feeding guild.

Old maple logs (OM) had the most specimens collected followed by old beech (OB), young beech (YB) and young maple (YM) (Table 2). The diversity (rarefaction estimate) was higher in young maple than old maple. On beech, diversity did not significantly differ between old and young wood. The Simpson’s index was lower in old maple and young beech than in young maple and old beech.

The results from the Generalized Linear Model (GLM) showed that decay stage and tree species had a combined effect on species abundance (Table 3). However, GLM did not retain any
significant model \( (P < 0.05) \) for species richness, estimated species richness (Chao) and Simpson’s diversity index.

**Community Composition**

Based on the Adonis, decay stages and tree species had significant effect on community composition. The four treatments were significantly different (Adonis \( R^2 = 0.21, P = 0.007 \)) in species assemblages and the NMDS results demonstrate that young decay stages are more variable in community composition than older decay stages (Fig. 4). Therefore, every decay stage and tree species has a distinct community composition, although decay stage and tree species only explain 21% of the variation.

Co-occurrence at the treatment level showed no difference from that expected by chance \( (P \geq 0.05) \), in maple, beech and early decay stage, although the community in the advanced decay stage exhibited high species segregation \( (P_{\text{observed} > \text{expected}} = 0.015) \).

**Discussion**

As expected, host-tree species and decay stage impact community composition and community assembly of saproxylic Diptera when examined at the species level and community assemblages in both tree species and decay stage are distinct. Therefore, to retain the highest diversity of dipterans in a forest, a variety of decaying wood species at different stages of decomposition is necessary. Decay stage also has a significant effect on abundance of Diptera; as the age of the decaying wood increases so does the abundance of Diptera, and the number of indicator species. These patterns are discernible in later decay stage and in the interactions between log type and decay stage. Additionally there is significant spatial segregation of species at later decay stages.

What was unexpected, however is that Diptera communities may be driven by different
processes. The above mentioned results suggest that deterministic processes drive Diptera community assembly at later stages of wood decay. However, stochastic processes are driving community assembly in early decay stage wood because community composition is more variable in early decay stages than later decay stage. Therefore, both stochastic and deterministic processes seem to play a role in community assembly in this system at different ages of wood decay.

Our results show that high species turnover was present among individual logs. These results are consistent with the other species specific study of North American Diptera (Work & Hibbert 2011), which observed compositional similarity between logs as low as 20 %. Coarse woody debris has been shown to be important at the stand level (e.g. landscape scale; Work et al. 2004). However, based on our results, we suggest that the scale of the log is essential for microhabitat diversity, which may be due to saproxylic Diptera having relatively poor active dispersal capabilities (Schiegg 2000) and specific microhabitat requirements (Siitonen 2012). The patchiness in assemblage pattern suggests that to develop comprehensive biomonitoring and biodiversity conservation strategies, research must focus on several scales and provide a maximum of decaying tree host species at different stages of decay.

The species of the decaying log is somewhat important in determining the community assembly of Diptera. Our results show that there are seven indicator species found to be specific to a tree species when interacting with decay stage and an additional three were found to be specific to one of the tree species no matter the decay. Having indicator species is in contrast with Irmler et al. (1996), Rotheray et al. (2001) and Persson et al. (2013) who found no influence of tree species on Coleoptera communities, which could be due to the difference in taxon grouped studied. Unlike Coleoptera and fungi (Persiani et al. 2010), few Diptera species feed
directly on wood (Teskey 1976); However, other factors, like decay stage not affected by tree
species, also affect community composition.

Based on our results, age of CWD has an important influence on the Diptera community
assembly. Late decay stage logs have a more distinct (10 indicator species no matter the tree
species and five specific to decay and tree species) and less variable community than early decay
logs (only two indicator species specific to both decay stage and tree species). This is potentially
due to changes in characteristics of the decaying wood as suggested by Persson et al. (2013).

Persson et al. (2013) concluded that microarthropods community changes as the physical and
chemical characteristics of the wood change. Unlike other studies of Coleoptera (Jonsell et
al. 2007) and midges (Irmler et al. 1996), we did not observe an increase in species richness with
age of log decomposition. A potential reason could be because of the differences in age of the
decaying logs observed in our study (four years between young logs and old logs) compared to
differences in ages of CWD in the other studies. We did, however, see higher Diptera abundance
in advanced decay logs, which allows us to conclude that the conditions of older logs can support
a higher number of individuals. A potential reason for the higher abundance in old logs could be
the increased presence of fungi, nitrogen, and water content and decreased carbon content in
aging wood (Hövemeyer & Schauermann 2003; Palviainen et al. 2010). Advanced stage decay
logs, therefore, provide more readily available food sources and ovipositing resource to
saprophagous and fungivorous Diptera (e.g. Milichiidae and Mycetophilidae; Buxton 1960;
Jakovlev 2011) than early stage decay logs and can, in turn, support higher abundances of
predatory species in families such as the Empididae.

The indicator species from our study represent a variety of feeding guilds (fungivore,
saprophage and predator). We can only speculate on specific feeding specialization and dispersal
capabilities of each species collected because there is sometimes not enough life history information on these species in the literature. Increased studies of life history in North American Diptera in CWD would, in part, start explaining the stochastic community assembly in young logs and the deterministic nature of Diptera communities in old logs.

The change in community structure in our study suggests that both stochastic and deterministic processes are occurring; however, the significance of each of the processes depends on the time of observation during the ecological succession. Newly fallen logs are likely to be colonized by many Diptera species through random events, because community composition is more variable in young decay stage. Even though Gossner et al. (2013) experimentally determined that there is a higher diversity of coleopteran guilds in fresh deadwood over older deadwood, Stockland (2012) states that tree specialists are expected in recently dead trees. As decaying wood ages, the assemblage of the community becomes much more specific and spatial segregation arises leading us to conclude that community assembly in older logs is driven by deterministic processes associated to decay and not as much to host tree species. Our NMDS results and the number of indicator species compared between the two stages of wood decay show that later decay stages are dominated by species that are specialised to live on or in older decaying wood.

Due to the temporal pattern apparent in our results, we suggest that future studies could profitably look more deeply into the continuum between stochastic and deterministic community assembly and place their analyses into a niche /neutral model framework. An interesting long-term experiment would be to control the age of logs by following community assembly from the moment a log is cut through its decay to determine at which moment the switch between stochastic and deterministic process occurs. Further studies are also needed to assess the
mechanisms driving the spatial segregation among species in old logs: resource utilization, interspecific competition, time (phenology) partitioning or space (where they are found in or on the logs) partitioning (Diamond 1975; Loreau 1989; Gilbert et al. 2008). Moreover, with the morphospecies approach we were able to obtain finer scale identification, but to fully understand community assembly patterns, more identification tools (including molecular techniques) of the broader community (including all invertebrates and fungi) and in-depth life-history information are needed. Finally, more data on the logs characteristics themselves would be beneficial to determine the interactions between all members in the CWD system.

Conclusion

Our results support recent studies that have demonstrated that both stochastic and deterministic processes drive community assembly (Gravel et al. 2006; Thompson and Townsend 2006; Ellwood et al. 2009; Barber and Marquis 2011; Ferrenberg et al. 2016; Grégoire Taillefer & Wheeler, 2017). Ellwood et al. (2009) observed that when environmental conditions were controlled for arthropods in tropical bird’s nest ferns the community assembly was stochastic. However, when they analysed different communities that were from two heights or successional stages, they determined that the communities were structured deterministically. Similarly, Thompson and Townsend (2006) demonstrated that both dispersal process and environmental conditions together explained patterns of local community assembly in stream invertebrates. These studies suggest that natural communities fall within a continuum between dispersal-assembly models, which are stochastic processes of community assembly, and niche models, which are deterministic processes.
Acknowledgments

We thank Duncan Selby, whose M.Sc. project on saproxylic gall midge diversity provided the Diptera specimens for this study and Kathrin Sim for reading a draft version. McGill University, Martin Lechowicz and Benoit Hamel provided access and logistic support at McGill University’s Gault Reserve at Mont Saint-Hilaire. Jon Gelhaus and Chris Borkent confirmed identifications of Tipulidae and Mycetophilidae, respectively. This research was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to TAW.
References


Supplemental materials

Supplemental figure 1 (.pdf): Map of Mont Saint-Hilaire Biosphere Reserve in Southern Quebec, Canada (45°32’40”N, 73°9’5”W). Google maps; topo map: 31 H/11 1:50,000.

Supplemental table (.xlsx): Raw data table of the specimens collected including species names, their species code, trophic group and abundance per log used for the analyses of saproxylic Diptera community assembly in southern Quebec. SA = saprophagous, FU = fungivorous, PR = predator, PA = parasitic, PH = phytophagous, OM = omnivorous, YM = young maple, OM = old maple, YB = young beech, OB = old beech.
Table 1. Southern Quebec decaying wood Saproxylic Diptera indicator species analysis showing species with a significant association ($P < 0.05$) with treatments and an indicator value $> 45$.

Table 2. Number of individuals (N), rarefaction estimates of species richness ($S_{est}$) (species ± SE, standardized at 445 individuals), Simpson’s diversity index and Chao index of saproxylic Diptera in decaying wood in each treatment.

Table 3. Summary of generalized linear models (GLM) showing the effect of environmental variables (decay stage and tree species) on saproxylic Diptera abundance in decaying logs in southern Quebec. Bold writing signifies the model with the lowest AIC value.
Figures

Figure 1. Decaying wood saproxylic Diptera trophic structure depending on feeding guild for A) abundance and B) species richness. Fungivores (FU), predators (PR), parasites (PA) and saprophages (SA).

Figure 2. Rarefaction estimates of expected species richness (±1 SE) of Diptera plotted against number of individuals at different wood decay stages and tree species. Young maple (YM), old maple (OM), young beech (YB) and old beech (OB).

Figure 3. Species accumulation curve of southern Quebec saproxylic Diptera. The bars indicate the 95% confidence interval based on standard deviation.

Figure 4. Non-metric multidimensional scaling ordination (stress = 0.088) based on Hellinger transformed abundance of saproxylic Diptera species in decaying wood in southern Quebec. The two axes of a two-dimensional solution are plotted. Ellipses represent community composition in young maple (YM), old maple (OM), young beech (YB) and old beech (OB).
Table 1 (on next page)

Southern Quebec decaying wood Saproxylic Diptera indicator species analysis showing species with a significant association ($P < 0.05$) with treatments and an indicator value $> 45$. 

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Indicator Value</th>
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<tbody>
<tr>
<td>Species A</td>
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<tr>
<td>Species B</td>
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<tr>
<td>Species C</td>
<td>48</td>
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<tr>
<td>Species D</td>
<td>49</td>
</tr>
<tr>
<td>Species E</td>
<td>50</td>
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(continued on next page)
Table 1. Southern Quebec decaying wood Saproxylic Diptera indicator species analysis showing species with a significant association ($P < 0.05$) with treatments and an indicator value $> 45$.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Trophic group</th>
<th>Species</th>
<th>Indicator value</th>
<th>$P$-value</th>
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<td>Maple</td>
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<td>Discobola annulata (Limoniidae)</td>
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<td>Saprophage</td>
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<td>0.015</td>
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<tr>
<td>Old Beech</td>
<td>Fungivore</td>
<td>Sciara sp. jm 7 (Sciaridae)</td>
<td>45</td>
<td>0.047</td>
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<td>Saprophage</td>
<td>Gaurax atripalpus (Chloropidae)</td>
<td>60</td>
<td>0.038</td>
</tr>
<tr>
<td>Young Maple</td>
<td>Parasite</td>
<td>Allophorocera sp. jm (Tachinidae)</td>
<td>60</td>
<td>0.031</td>
</tr>
</tbody>
</table>
Table 2 (on next page)

Sample size, estimates and diversity indices of saproxylic Diptera in decaying wood in each treatment.

Number of individuals (N), rarefaction estimates of species richness ($S_{est}$) (species ± SE, standardized at 445 individuals), Simpson’s diversity index and Chao index.
Table 2. Number of individuals (N), rarefaction estimates of species richness ($S_{est}$) (species ± SE, standardized at 445 individuals), Simpson’s diversity index and Chao index of saproxylic Diptera in decaying wood in each treatment.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>$S_{est}$</th>
<th>Simpson</th>
<th>Chao</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young Maple</td>
<td>445</td>
<td>113 ± 0</td>
<td>41.5</td>
<td>91.6 ± 6.3</td>
</tr>
<tr>
<td>Old Maple</td>
<td>1066</td>
<td>72 ± 3.9</td>
<td>5.7</td>
<td>90.3 ± 9.6</td>
</tr>
<tr>
<td>Young Beech</td>
<td>698</td>
<td>81 ± 3.2</td>
<td>7.3</td>
<td>84.6 ± 6.3</td>
</tr>
<tr>
<td>Old Beech</td>
<td>825</td>
<td>87 ± 3.8</td>
<td>21.3</td>
<td>92.8 ± 9.4</td>
</tr>
</tbody>
</table>
Table 3 (on next page)

Summary of generalized linear models (GLM) showing the effect of environmental variables (decay stage and tree species) on saproxylic Diptera abundance in decaying logs in southern Quebec.
Table 3. Summary of generalized linear models (GLM) showing the effect of environmental variables (decay stage and tree species) on saproxylic Diptera abundance in decaying logs in southern Quebec. Bold writing signifies the model with the lowest AIC value.

<table>
<thead>
<tr>
<th>Formula</th>
<th>AIC</th>
<th>Residual degrees of freedom</th>
<th>Residual deviance</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>abun ~ decay</td>
<td>1216.6</td>
<td>18</td>
<td>1082</td>
<td>1267.5</td>
</tr>
<tr>
<td>abun ~ tree</td>
<td>1402.1</td>
<td>18</td>
<td>1267.5</td>
<td>1267.5</td>
</tr>
<tr>
<td>abun ~ decay * tree</td>
<td><strong>1124.1</strong></td>
<td>16</td>
<td>985.5</td>
<td>1267.5</td>
</tr>
<tr>
<td>abun ~ decay + tree</td>
<td>1218.6</td>
<td>17</td>
<td>1082</td>
<td>1267.5</td>
</tr>
</tbody>
</table>
Figure 1 (on next page)

Decaying wood saproxylic Diptera trophic structure depending on feeding guild for A) abundance and B) species richness.

Fungivores (FU), predators (PR), parasites (PA) and saprophages (SA)
Figure 2 (on next page)

Rarefaction estimates of expected species richness (±1 SE) of Diptera plotted against number of individuals at different wood decay stages and tree species.

Young maple (YM), old maple (OM), young beech (YB) and old beech (OB).
Figure 3 (on next page)

Species accumulation curve of southern Quebec saproxylic Diptera.

The bars indicate the 95% confidence interval based on standard deviation.
Figure 4 (on next page)

Non-metric multidimensional scaling ordination (stress = 0.088) based on Hellinger transformed abundance of saproxylic Diptera species in decaying wood in southern Quebec.

The two axes of a two-dimensional solution are plotted. Ellipses represent community composition in young maple (YM), old maple (OM), young beech (YB) and old beech (OB).