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Abstract

The adult caddisfly assemblages of Drummond Island, a Michigan island in Lake Huron near the Canadian border, were sampled in 2021–2022 from 3 sites on Lake Huron, 8 inland lakes, 2 vernal pools, and 1 stream. Adult caddisflies from each site were sampled in spring, summer, and autumn using ultraviolet blacklight traps. A total of 89 species representing 37 genera and 12 families was collected, including several not seen in Michigan for 50–70 years and the first confirmation of the rare species *Beothukus complicatus* (Banks) (Phryganeidae) from the state. A non-metric multidimensional scaling ordination determined distinct species assemblages between lakes, vernal pools, and the stream, but no difference between inland lakes and Lake Huron sites. Based on total organic biomass, all 4 habitat types were dominated (60–90%) by shredders, particularly those in the family Phryganeidae. Total species richness was lower on Drummond Island than within other Michigan areas where rigorous recent sampling has occurred, possibly due to it being an isolated island. This study provides some of the first data on the caddisfly assemblages of undisturbed lakes in a Nearctic temperate environment, and demonstrates the importance of caddisfly shredders in lake habitats.

Keywords: Michigan, Trichoptera, lake, assemblage, biomass, Phryganeidae

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Several recent studies have documented large-scale declines in aquatic insect species and fundamental changes to their community ecology (Sánchez-Bayo and Wyckhuys 2019, Baranov et al. 2020, van Klink et al. 2020, Houghton and DeWalt 2023). Without reference sites or historical data for comparison, however, it is difficult to accurately evaluate current species composition or ecological functioning of freshwater ecosystems. This problem is especially true for lake ecosystems, as research on the biotic assemblages and potential for anthropogenic disturbance of such habitats has lagged far behind that of river habitats (Peck et al. 2020, Fergus et al. 2021). Therefore, quantifying assemblages of ecologically important aquatic insect taxa, especially those of lakes, should be a scientific priority.

The caddisflies (Trichoptera) constitute a particularly important group of aquatic organisms due to their overall abundance, high species richness, high ecological diversity, and differing sensitivities to various anthropogenic disturbances (Barbour et al. 1999, Dohet 2002, Morse et al. 2019a, Houghton and DeWalt 2021). Although the caddisflies of Michigan are generally well known (Houghton et al. 2018a, Houghton et al. 2022), most collections of the taxonomically important adult stage have consisted of a single sample from a collection site, usually an ultraviolet light trap deployed for a single evening. To accurately capture the characteristic species richness and ecological functioning of Michigan ecosystems, multiple samples need to be taken from different seasons within a variety of habitats in an undisturbed area. Recent area-specific studies of Michigan habitats have yielded new species, new state records, and recaptures of species not collected since the 1940s (DeWalt and South 2015; Houghton 2016, 2021b, 2022; Houghton and Haack 2023). Thus, additional interesting species and records almost certainly remain undiscovered in under-collected regions of the state.

While many studies of aquatic insect assemblages have focused on the benthic larval stage, several obvious problems exist when doing so. First, the success of sampling benthic specimens is highly dependent on sampling effort (Cao et al. 2002) and the specific sampling device used. Many common benthic collecting devices such as kick nets, Hess samplers, and Surber samplers, over-emphasize shallow habitats with uniform substrate, while under-sampling large woody debris, the undersides of large boulders, bank habitats, near-shore vegetation, and the entire hyporheic zone (Gerth and Herily 2006, Chessman et al. 2007, Cao and Hawkins 2011). Deep water habitats, such as those of lakes, are particularly difficult to sample, much less so with any level of standardization (Cao and Hawkins 2011). Second, most larvae are not identifiable to the species level, resulting in a loss of information and decreased metric sensitivity (Hawkins et al. 2000, Stribling et al. 2008, Houghton et al. 2018b). Third, the collection of a pre-emergent specimen does not confirm its ability to complete its entire life cycle in a particular habitat, thus its capture—especially that of a subterminal instar—may yield erroneous information about that habitat. All of these problems can be overcome by sampling the winged adult stage, particularly that of the caddisflies, since specimens are attracted to ultraviolet lights regardless of their functional feeding group or specific natal microhabitat, and the presence of emergent adults confirms the completion of the entire life cycle (Houghton 2004, Wright et al. 2013, Brakel et al. 2015). Moreover, while the exact area sampled by an ultraviolet light is not known, it almost certainly is many times larger than that of multiple samples of typical benthic sampling devices (Houghton and DeWalt 2021). Thus, while benthic sampling is a valuable technique for stream bioassessment, sampling adult aquatic insects is likely a more accurate representation of habitat conditions, assuming that specimens are captured near their actual natal habitat.

Drummond Island is located in northern Lake Huron at the eastern end of Michigan's Upper Peninsula, 1 km from the Canadian border, and 2–3 km from nearby Canadian islands (Fig. 1). The island has an area of 33,642 ha—58% of which is included in the Lake Superior State Forest—224 km of coastline, and 36 inland lakes (Haack 2020). Limestone and dolomite form the bedrock of Drummond Island, which is frequently exposed at the surface where it forms broad, flat expanses known as alvars that have minimal soil and are dominated by grasses and sedges (Lincoln 2018).

Several insect surveys have been conducted on Drummond Island in the past few decades, with most concentrating on insects inhabiting the Maxton Plains alvar and other limestone communities. These surveys have focused on Hemiptera, including Homoptera (Albert et al. 1994, Albert et al. 1995, Hamilton 1994, Hamilton 1998, Spencer et al. 2018), Lepidoptera (Albert et al. 1994, Albert et al. 1995), Odonata (Albert et al. 1994, Albert et al. 1995), Orthoptera (Albert et al. 1995), and wood-boring Coleoptera and Hymenoptera (Haack 2020). To date, there have been no surveys of the caddisflies on the island. The primary objective of our study was to construct a preliminary list of caddisfly species on Drummond Island through seasonal sampling of multiple sites, with an emphasis on inland lentic habitats and the Lake Huron shoreline. A secondary objective was to compare species assemblages and functional feeding group biomasses from different habitat types.

Materials and Methods

A total of 14 sites on Drummond Island were sampled for adult caddisflies: 3 sites along the shoreline of Lake Huron, 8 inland lakes, 2 vernal pools, and 1 stream (Table 1, Fig. 1). Sites were chosen to reflect a variety of habitats (Fig. 2) that also had reasonable road access. Sites were generally undisturbed and had local (Hydrologic Unit Code-12) catchment habitat composed of 90–99% native plant communities. All of the inland lakes were undammed except for Pigeon Cove Lake, which was a 30–40-ha flooding area. Other inland lakes averaged 1–2 m in depth and ranged in size from 5–125 ha (Table 1), with mostly silt and marl bottoms, and abundant shoreline and littoral vegetation (Fig. 2). All of our sites were within 20 km of each other. Most were separated by 1–10 km.

Eight inland lakes, the single stream, and 3 Lake Huron sites were sampled in June and September 2021, and again in May 2022. In 2022, samples were taken in June, July, August, September, and October from 1 Lake Huron site, 1 inland lake, and 2 vernal pools (Table 1). Each sample consisted of a 15-watt portable ultraviolet light (BioQuip, Rancho Domingo, CA, model 2805) placed over a white 34 × 25 cm pan filled with 80% ethanol. Lights were placed within 1 m of the shoreline on the ground, or slightly elevated (~50 cm) when the nearby herbaceous vegetation was tall, or placed on a dock within 2–3 m of the shoreline when available. Lights were turned on 30–90 minutes before dusk and collected 90–135 minutes after dusk (Wright et al. 2013). May–July samples were collected only if the peak daytime temperature was >25 °C, dusk temperature was >18 °C, and there was minimal wind and no precipitation at dusk (Houghton 2004). During the cooler months of September and October, samples were collected if daytime temperature was >20 °C and dusk temperature was >16 °C. In 2021 and May 2022, sampling occurred at 6 sites per evening, usually on consecutive days or as weather conditions allowed. For the later 2022 samples, all 4 sites were sampled on the same evening. Since aquatic insects collected

Table 1. The 8 inland lakes, 3 sites of Lake Huron, 1 stream, and 2 vernal pools sampled on Drummond Island during 2021 and 2022. Area was estimated by measuring each inland lake using the 'Ruler: Polygon' feature of Google Earth. Habitat: the percentage of a site's primary catchment classified as forest, grassland, or wetland based on the USEPA StreamCat database (https://watersgeo.epa.gov/watershedreport), accessed November 2021 (Hill et al. 2016). Month abbreviations: Ma = May, Jn = June, Jl = July, Au = August, Sp = September, Oc = October.

Site	Name	Latitude	Longitude	Elevation (m)	Area (ha)	Habitat	Dates sampled
1	Lake Huron, Sims Point	46.0197	–83.8275	177	N/A	93%	Jn, Sp 21, Ma 22
2	Lake Huron, Fairview Cove	45.9578	–83.8433	177	N/A	93%	Jn, Sp 21; Ma, Jn, Jl, Au, Sp, Oc 22
3	Lake Huron, Potagannissing Bay	46.0347	–83.6753	177	N/A	98%	Jl, Sp 21, Ma 22
4	Vernal pool #1	45.9564	–83.8431	181	N/A	93%	Jn, Jl, Au, Sp, Oc 22
5	Vernal pool #2	45.9572	–83.8367	187	N/A	93%	Jn, Jl, Au, Sp, Oc 22
6	Stringham Lake	46.0019	–83.8405	184	28	93%	Jn, Sp 21, Ma 22
7	Parish Lake	45.9778	–83.8525	177	30	93%	Jn, Sp 21, Ma 22
8	Seaman Lake	45.9636	–83.8303	180	10	93%	Jn, Sp 21; Ma, Jn, Jl, Au, Sp, Oc 22
9	Pigeon Cove Lake	45.9811	–83.8103	180	30–40	90%	Jn, Sp 21, Ma 22
10	Helen Lake	45.9544	–83.7547	178	10	93%	Jn, Sp 21, Ma 22
11	Nasi Lake	45.9847	–83.6836	200	5	97%	Jn, Sp 21, Ma 22
12	First Lake	46.0414	–83.6547	178	125	98%	Jl, Sp 21, Ma 22
13	Dickenson Lake	45.9461	–83.5702	193	88	99%	Jl, Sp 21, Ma 22
14	Pigeon Cove Creek	45.9778	–83.8092	181	N/A	90%	Jn, Sp 21, Ma 22

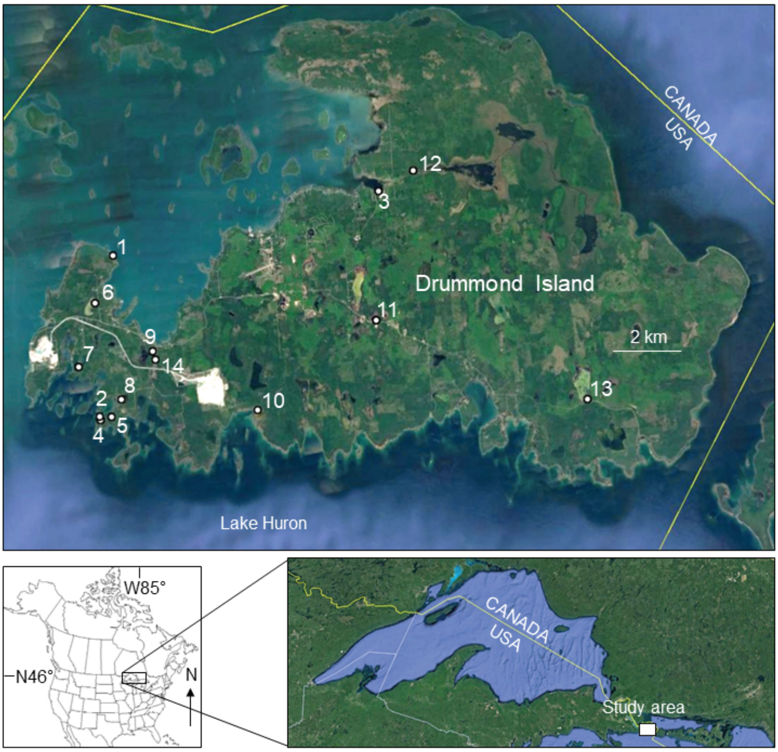

Figure 1. The sampling area and our 14 sampling sites of Drummond Island, MI. Site numbers correspond to Table 1. Base maps ©Google, TerraMetrics

within 100 m of a habitat generally reflect the assemblage of that habitat (Sode and Wiberg-Larson 1993, Peterson et al. 1999, Sommerhäuser et al. 1999, Calor and Mariano 2012, Brakel et al. 2015, DeWalt and South 2015, Houghton et al. 2018b, Pereira et al. 2020, Houghton 2022), dispersals of adults between sites, while possible, were considered unimportant to our analyses.

All male and female specimens, except for some non-identifiable females of the family Hydroptilidae, were identified using Houghton's (2012) treatment of the Minnesota caddisflies or with more specific taxonomic treatments as needed. Specimens were coded with their affinity for 1 of 6 different functional feeding groups (FFGs) based on Morse et al. (2019b) and Houghton (2021a): algal piercers, filtering collectors, gathering collectors, predators, scrapers, and shredders. Codes consisted of '0' for no affinity for a FFG, '1' low affinity, '2' moderate affinity, '3' high affinity, and '4' near exclusive affinity (Chevenet et al. 1994) (Table 2). These codes were converted to proportions: 0 = 0.0, 1 = 0.25, 2 = 0.50, 3 = 0.75, and 4 = 1.0, to multiply by the estimated biomass for each species (Beauchard et al. 2017). All species within a genus were coded the same. This approach more accurately reflected the feeding plasticity of aquatic insects than pure categorization (Dolédec et al. 2000, Gayraud et al. 2003, Tomanova et al. 2007).

Ash-free dry mass (AFDM) values for specimens was estimated based on Houghton and Lardner (2020) (Table 2). Genera without a determined value were assigned the value of a genus of similar body size. All species within a genus were assigned the same value. While this approach did not reflect differences in body size due to differences in sexual dimorphism, interspecific size differences, specific habitat, larval food quality, or emergence timing, among other differences (Svensson 1975; Wagner 2002, 2005), it still allowed for a more precise determination of FFG differences between sites than simply counting specimens and treating them as ecologically equivalent (Houghton and Lardner 2020, Venarsky et al. 2020). All determined specimens have been deposited in the Hillsdale College Insect Collection (HCIC).

Figure 2. Representative habitats of Drummond Island. A: Fairview Cove of Lake Huron (Site 2), B: First Lake (12), C: Pigeon Cove Lake flooding area (9), D: Dickenson Lake (13), E: Pigeon Cove Creek (14), F: Vernal pool #2 (5). Site numbers correspond to Table 1 and Figure 1.

To delineate differences between caddisfly assemblages of different habitat types, specimens were examined with a non-metric multidimensional scaling (NMDS) ordination using the program PC-ORD v.7 for Windows (Peck 2016). To reflect a consistent sampling effort for each site, the data matrix included the total combined specimen abundance per site for 1 summer (late June to mid-July) sample and 1 fall (early to mid-September) sample. Total specimen abundance data were $\log_{10}$ (x + 1) transformed before analysis. All species were weighted equally. The NMDS ordination was conducted using the default program settings, 250 randomized runs, and a Bray-Curtis distance measure. A Monte Carlo test was conducted on each determined axis to assess its difference from a random ordination structure (Dexter et al. 2018). Coefficients of determination (r^2) for the associations between ordination distances and the original n-dimensional space distance were also determined in PC-ORD using a Bray–Curtis distance measure (Peck 2016). This analysis calculated the percentage of variance explained by each

Table 2. Ash-free dry mass (AFDM) and functional feeding group (FFG) affinity coding data for species of the 37 caddisfly genera collected from Drummond Island. Genera are arranged alphabetically. AFDM data from Houghton and Lardner (2020). Genera denoted with an asterisk were assigned the AFDM value of a genus of similar body size. FFG affinities from Morse et al. (2019b) and Houghton (2021a). FC = filtering collector, GC = gathering collector, Pi = algal piercer, Pr = predator, Sc = scraper, Sh = shredder.

		FFG affinity codes					
Genus	**AFDM**	**FC**	**GC**	**Pi**	**Pr**	**Sc**	**Sh**
Agarodes	0.795	0	2	0	0	0	2
Agraylea	0.029	0	2	2	0	0	0
Agrypnia	3.059	0	0	0	0	0	4
Anabolia	2.413	0	1	0	0	0	3
Banksiola	1.371	0	0	0	1	0	3
*Beothukus**	3.059			unknown			
Ceraclea	0.695	0	2	0	1	0	1
Cheumatopsyche	0.346	4	0	0	0	0	0
*Fabria**	3.059	0	0	0	0	0	4
*Glyphopsyche**	2.413			unknown			
*Hagenella**	3.059			unknown			
Helicopsyche	0.223	0	0	0	0	4	0
*Holocentropus**	0.418	1	0	0	3	0	0
Hydropsyche	0.392	4	0	0	0	0	0
Hydroptila	0.017	0	0	3	0	1	0
*Ithytrichia**	0.017	0	0	1	0	3	0
Lepidostoma	0.469	0	1	0	0	0	3
Leptocerus	0.235	0	1	0	0	0	3
Limnephilus	1.549	0	1	0	0	0	3
Molanna	0.715	0	1	0	1	2	0
Mystacides	0.321	0	3	0	0	0	1
Nectopsyche	0.594	0	1	0	1	0	2
Nemotaulius	5.515	0	0	0	0	0	4
Nyctiophylax	0.105	1	0	0	2	0	1
Oecetis	0.452	0	0	0	3	0	1
Orthotrichia	0.011	0	0	4	0	0	0
*Oxyethira**	0.011	0	1	3	0	0	0
Phryganea	6.846	0	0	0	1	0	3
*Phylocentropus**	0.418	4	0	0	0	0	0
Platycentropus	3.973	0	0	0	0	0	4
*Plectrocnemia**	0.418	1	0	0	3	0	0
Polycentropus	0.418	1	0	0	3	0	0
Psychomyia	0.038	0	3	0	0	1	0
Ptilostomis	7.217	0	0	0	1	0	3
Pycnopsyche	2.199	0	0	0	0	1	3
Setodes	0.192	0	3	0	1	0	0
Triaenodes	0.595	0	1	0	0	0	3

determined NMDS axis in the calculated distance matrix. Differences in mean biomass for each FFG between lakes and streams were determined using non-parametric Mann-Whitney *U*-tests and a standard alpha level of 0.05. The stream and vernal pool habitats were not analyzed due to low sample size. A species accumulation curve based on all species and samples collected was produced using the program EstimateS for Windows v. 9.1 (https://www.robertkcolwell.org/pages/estimates). Similar curves were produced for caddisflies collected from the Huron Mountains (Houghton 2022) and the Black River Ranch (Houghton 2016), two other areas of northern Michigan recently sampled with a rigorous effort.

Results

A total of 5567 caddisfly specimens were collected and identified from our 56 ultraviolet light trap samples, representing 89 species, 37 genera, and 12 families

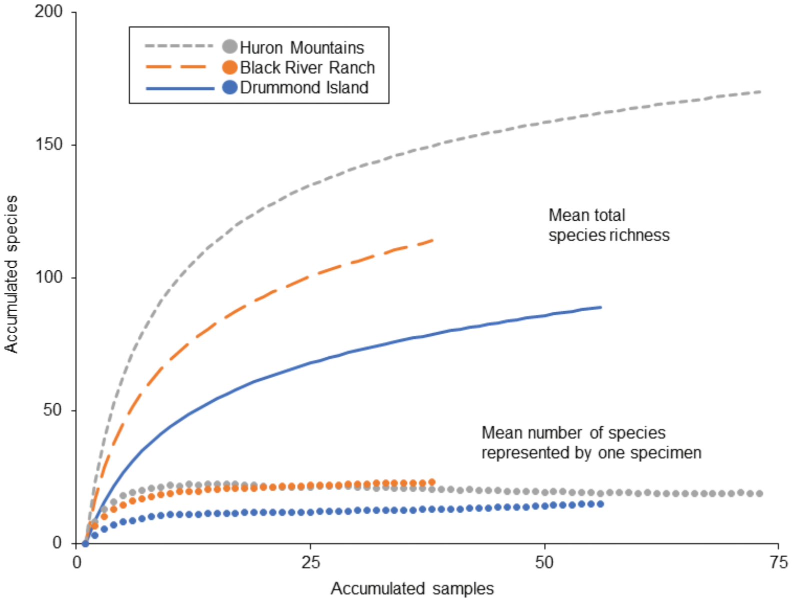

Figure 3. Mean total species richness (lines) and number of species represented by a single specimen (circles) based on all 56 blacklight samples collected from Drummond Island, in comparison to those from the Huron Mountains (Houghton 2022) and Black River Ranch (Houghton 2016) areas of northern Michigan. For graphs, 100 randomized combinations of sample order were calculated and then a mean value determined and displayed.

(Table 3). Leptoceridae (22), Hydroptilidae (19), Limnephilidae (12), and Phryganeidae (12) were the most species-rich families. *Banksiola crotchi* Banks (Phryganeidae) and *Oecetis inconspicua* (Walker) (Leptoceridae) were found at all 14 sites. Those two species (1148 and 729 specimens, respectively) were also the most abundant among all sites, along with *Plectrocnemia cinerea* (Hagen) (Polycentropodidae) (436) and *Agraylea multipunctata* Curtis (Hydroptilidae) (365). The calculated species accumulation curve for Drummond Island exhibited lower species richness relative to sampling effort than did those from the Huron Mountains or the Black River Ranch (Fig. 3). None of the three curves approached an asymptote.

Of the top 10 species with the greatest total AFDM, 6 were in the family Phryganeidae, including the top 4 (Table 3). Species of that family constituted nearly 2/3 of the total AFDM of the entire caddisfly assemblage sampled. *Banksiola crotchi* (1573 mg) by itself composed over 25% of the total assemblage AFDM, and had more than double that of *Phryganea cinerea* Walker (Phryganeidae) (609 mg), the species with the second greatest AFDM.

An NMDS ordination of summer and fall species assemblages for all sampling sites produced a two-dimensional solution explaining almost 60% of the variation in the data set (Fig. 4). Lake, stream and vernal pool habitats were distinct from each other with no overlap, but inland lake and Lake Huron habitats were not distinct from each other. All habitat types were dominated by shredders, which encompassed 60–90% of mean total assemblage AFDM (Fig. 5). There was no significant difference in mean AFDM of each individual FFG between inland lakes and Lake Huron sites based on nonparametric Mann-Whitney *U*-tests (Fig. 5).

Discussion

Although our sample size within different habitat types was small, the separation of caddisfly species assemblages between lakes, vernal pools, and the stream despite their close geographic proximity supports the distinctiveness of the different habitat types. Houghton (2022) found similar distinctiveness between lake and stream habitats of Michigan's Huron Mountains, an area about 300 km west of Drummond Island. Predictably, Drummond Island lake assemblages were dominated by known len-

Table 3. The 89 caddisfly species collected at Drummond Island habitats in 2021 and 2022 from our 56 blacklight samples. Taxa are arranged taxonomically by family and genus. Number of species within each family in parentheses. Site numbers correspond to Table 1 and Figure 1. Locs = total localities where a species was found. Spcs = total number of specimens of a species collected from all habitats. AFDM : total ash-free dry mass from all sites combined. Hu = shoreline sites of Lake Huron, VP = vernal pools, IL = inland lakes, St = stream.

	Site number																
	Hu			VP		IL								St			
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**Locs**	**Spcs**	**AFDM**
DIPSEUDOPSIDAE (1)																	
Phylocentropus placidus (Banks) 1905	0	2	6	2	0	0	0	2	1	0	1	0	0	0	6	14	5.9
HELICOPSYCHIDAE (1)																	
Helicopsyche borealis (Hagen) 1861	38	134	0	5	3	0	0	1	3	4	0	1	0	4	9	193	43.0
HYDROPSYCHIDAE (6)																	
Cheumatopsyche analis (Banks) 1908	0	0	0	1	0	0	0	1	0	0	1	180	0	21	5	204	70.6
Cheumatopsyche campyla Ross 1938	4	21	2	6	3	0	0	0	0	2	0	0	1	0	7	39	13.5
Cheumatopsyche oxa Ross 1938	0	0	0	0	0	0	0	0	0	0	0	0	0	12	1	12	3.0
Hydropsyche alternans (Walker) 1852	0	18	0	0	0	0	0	0	0	0	0	0	0	0	1	18	7.1
Hydropsyche betteni Ross 1938	1	1	2	0	0	0	0	0	0	0	0	0	0	0	3	4	24.0
Hydropsyche slossonae Banks 1905	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	14.5
HYDROPTILIDAE (19)																	
Agraylea multipunctata Curtis 1834	15	4	140	6	6	7	33	19	46	5	0	83	1	0	12	365	10.8
Hydroptila ampoda Ross 1941	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	4	0.1
Hydroptila armata Ross 1938	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	<0.1
Hydroptila hamata Morton 1905	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	2	<0.1
Hydroptila jackmanni Blickle 1963	2	0	2	0	0	0	0	0	0	0	0	0	0	0	2	4	0.1
Hydroptila metoeca Blickle & Morse 1954	0	1	0	14	3	0	0	0	0	0	0	0	0	0	3	18	0.2
Hydroptila novicola Blickle & Morse 1954	0	0	0	0	0	0	0	0	0	0	0	0	0	37	1	37	0.3
Hydroptila waubesiana Betten 1934	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	<0.1
Ithytrichia clavata Morton 1905	0	8	0	0	0	0	0	0	0	0	0	0	0	0	1	8	0.1
Orthotrichia baldufi Kingsolver & Ross 1961	0	0	7	0	0	0	0	2	5	0	0	0	0	0	3	14	0.2
Orthotrichia cristata Morton 1905	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	2	<0.1
Orthotrichia curta Kingsolver & Ross 1961	0	0	0	0	0	0	0	0	6	0	0	0	0	0	1	6	0.1
Oxyethira anabola Blickle 1966	0	0	0	0	0	0	0	0	24	0	0	0	0	0	1	24	0.3
Oxyethira forcipata Mosely 1934	0	0	4	0	0	0	0	0	0	0	0	0	0	0	1	4	<0.1
Oxyethira michiganensis Mosely 1934	0	0	1	0	0	0	0	0	0	0	0	2	0	0	2	3	<0.1
Oxyethira obtatus Denning 1947	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	<0.1
Oxyethira serrata Ross 1938	2	6	1	0	0	0	1	0	1	0	0	0	0	0	5	11	0.1
Oxyethira verna Ross 1938	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	3	<0.1
Oxyethira zeronia Ross 1941	0	0	5	0	0	11	2	0	27	0	0	0	0	0	4	45	0.5

(Continued on next page)

Table 3. (Continued).

	Site number																
	Hu			VP		IL								St			
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**Locs**	**Spcs**	**AFDM**
LEPIDOSTOMATIDAE (1)																	
Lepidostoma togatum (Hagen) 1861	4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	1.9
LEPTOCERIDAE (22)																	
Ceraclea alagma (Ross) 1938	0	0	113	0	0	0	0	3	0	0	0	13	0	0	3	129	89.6
Ceraclea cancellata (Betten) 1934	1	0	17	0	0	0	0	1	0	0	0	1	0	0	4	20	13.9
Ceraclea diluta (Hagen) 1861	1	3	1	1	0	0	0	0	0	0	2	0	0	0	5	8	5.5
Ceraclea maculata (Banks) 1899	0	0	31	0	0	0	0	0	2	0	0	0	0	2	3	35	23.9
Ceraclea resurgens (Walker) 1852	11	3	56	0	0	0	0	0	15	0	0	9	0	0	5	94	67.0
Ceraclea tarsipunctata (Vorhies) 1909	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.7
Ceraclea transversa (Hagen) 1861	0	10	1	4	0	0	0	2	0	0	1	0	0	0	5	18	12.5
Leptocerus americanus (Banks) 1899	0	0	104	1	0	0	0	20	0	0	1	53	0	0	5	179	42.0
Mystacides interjectus (Banks) 1914	0	1	5	1	0	2	190	42	0	0	4	17	24	0	9	286	91.8
Nectopsyche albida (Walker) 1852	6	0	0	0	0	0	8	1	0	1	0	0	0	0	4	16	9.5
Oecetis cinerascens (Hagen) 1861	2	2	25	1	1	0	17	9	1	1	0	16	3	1	12	79	35.7
Oecetis immobilis (Hagen 1861)	0	0	7	0	0	0	0	0	0	0	0	0	0	0	1	7	3.2
Oecetis inconspicua (Walker) 1852	19	3	24	10	3	77	89	274	38	76	83	5	23	5	14	729	329.7
Oecetis osteni Milne 1934	2	0	135	0	0	0	3	2	26	0	0	7	1	1	8	177	73.7
Oecetis persimilis (Banks) 1907	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0.4
Setodes oligius (Ross) 1938	2	0	0	0	0	0	0	1	0	0	0	0	0	0	2	3	0.6
Triaenodes aba Milne 1935	0	0	1	0	0	0	0	0	5	0	0	0	0	0	2	6	3.6
Triaenodes baris Ross 1938	0	0	0	1	0	0	1	0	1	0	1	0	1	0	5	5	3.0
Triaenodes dipsius Ross 1938	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0.6
Triaenodes injustus (Hagen) 1861	20	2	14	5	3	0	1	35	6	0	8	14	0	0	10	108	64.2
Triaenodes marginatus Sibley 1926	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1.2
Triaenodes tardus Milne 1934	0	0	8	0	0	0	2	14	0	0	0	0	0	0	3	24	14.3
LIMNEPHILIDAE (12)																	
Anabolia bimaculata (Walker) 1852	0	1	0	0	0	0	1	1	0	0	0	0	1	0	4	4	9.7
Glyphopsyche irrorata (F.) 1781	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	3.1
Limnephilus indivisus Walker 1852	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	2.3
Limnephilus moestus Banks 1908	0	2	0	2	1	0	0	3	1	0	0	7	0	7	7	23	35.6
Limnephilus ornatus Banks 1897	0	0	0	0	0	0	0	0	2	0	4	13	0	3	4	22	34.1
Limnephilus parvulus (Banks) 1905	0	0	0	0	0	0	0	0	1	0	2	1	0	0	3	4	6.2
Limnephilus sericeus (Say) 1824	1	1	0	19	2	0	1	0	1	0	0	0	0	0	6	25	38.7
Limnephilus submonilifer Walker 1852	1	1	0	64	14	0	2	1	0	0	0	4	0	11	8	98	151.8
Nemotaulius hostilis (Hagen) 1873	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	5.5

Platycentropus radiatus (Say) 1824	0	1	1	0	0	0	0	0	4	2	1	2	1	5	8	17	67.5
Pycnopsyche guttifera (Walker) 1852	1	16	0	2	3	0	1	2	0	3	0	0	1	12	9	41	90.2
Pycnopsyche lepida (Hagen) 1861	0	0	0	0	0	0	22	0	0	0	0	0	0	0	1	22	48.4
MOLANNIDAE (3)																	
Molanna flavicornis Banks 1914	2	0	0	0	0	1	0	0	0	0	0	0	0	0	2	3	2.1
Molanna tryphena Betten 1934	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	1.4
Molanna uniophila Vorhies 1909	0	0	5	0	0	0	10	0	0	1	0	8	7	0	5	31	22.2
PHRYGANEIDAE (12)																	
Agrypnia colorata Hagen 1873	5	2	0	0	0	0	0	67	2	1	0	6	4	0	7	87	266.1
Agrypnia improba (Hagen) 1873	2	0	9	0	1	0	0	7	46	36	12	5	3	13	10	134	409.9
Agrypnia straminea Hagen 1873	0	0	3	0	0	19	9	0	3	1	0	0	0	0	5	35	107.1
Agrypnia vestita (Walker) 1852	0	1	2	1	1	0	0	2	1	0	0	0	0	0	6	8	24.5
Banksiola crotchi Banks 1943	7	7	55	38	3	4	4	27	747	20	98	12	5	121	14	1148	1573.7
Beothukus complicatus (Banks) 1924	0	0	0	0	0	0	0	1	4	0	1	0	0	0	3	6	18.4
Fabria inornata (Banks) 1907	0	0	0	0	0	0	0	0	8	0	0	0	0	0	1	8	24.5
Hagenella canadensis (Banks) 1907	0	0	0	1	0	0	0	0	1	0	0	0	0	2	3	4	12.2
Phryganea cinerea Walker 1852	5	13	1	9	26	2	0	5	15	0	0	3	2	8	11	89	609.3
Ptilostomis angustipennis (Hagen) 1873	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	9.2
Ptilostomis ocellifera (Walker) 1852	0	0	0	0	1	1	0	0	0	0	0	0	1	0	3	3	21.7
Ptilostomis semifasciata (Say) 1828	13	15	0	1	2	0	1	3	7	19	1	0	4	0	10	66	476.3
POLYCENTROPODIDAE (10)																	
Holocentropus flavus (Banks) 1908	0	0	0	1	0	1	0	1	3	1	3	0	0	0	6	10	4.2
Holocentropus interruptus (Banks) 1914	0	3	11	2	0	0	6	1	2	7	0	0	0	0	7	32	16.4
Holocentropus melanae (Ross) 1938	0	0	0	0	0	1	0	0	6	0	0	0	0	9	3	16	2.7
Holocentropus milaca Etnier 1968	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0.2
Nyctiophylax affinis (Banks) 1897	24	14	0	34	31	0	0	2	1	7	0	18	1	0	9	132	13.9
Plectrocnemia albipuncta (Banks) 1930	1	0	0	3	0	0	0	0	37	0	0	0	0	6	4	47	7.8
Plectrocnemia cinerea (Hagen) 1861	113	126	24	41	8	0	3	37	5	29	2	33	15	0	12	436	182.1
Plectrocnemia remota Banks 1911	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0.4
Plectrocnemia weedi Blickle & Morse 1955	0	0	0	0	0	0	0	0	3	0	0	2	0	0	2	5	2.1
Polycentropus confusus Hagen 1861	3	13	0	14	0	0	0	1	0	0	0	0	0	0	4	31	5.1
PSYCHOMYIIDAE (1)																	
Psychomyia flavida Hagen 1861	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	<0.1
SERICOSTOMATIDAE (1)																	
Agarodes distinctus Ulmer 1905	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.8
Total species per site	29	34	39	31	20	11	23	33	43	18	18	27	19	24			
Total species per habitat type	Hu			VP		IL								St			
	60			34		65								24			

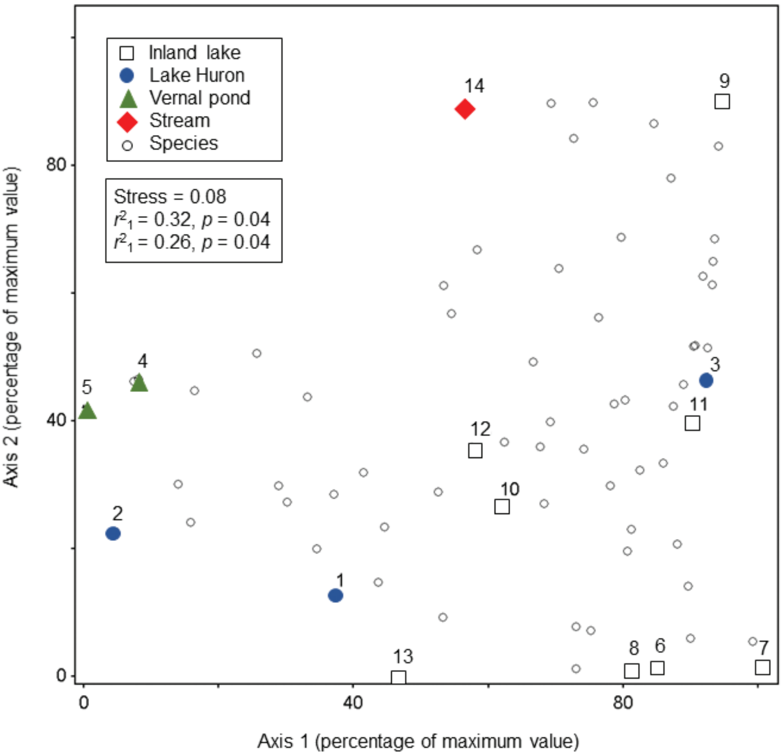

Figure 4. NMDS ordination of our 14 sampling sites based on caddisfly $\log_{10}$ abundance per species per site for 1 summer (late June to mid-July) and 1 fall (early to mid-September) blacklight sample for each site. *P*-values from a Monte Carlo test of non-random ordination structure. Site numbers correspond to Table 1 and Figure 1. Species labels omitted for clarity.

tiphilic leptocerid and phryganeid caddisflies (Wiggins 2004). The dominance of the latter family was especially noteworthy. Not only did phryganeids constitute a strong majority of assemblage biomass on Drummond Island, but 2/3 of all known Michigan phryganeid species were found during this study, including four species that are rarely collected from the state: *Agrypnia colorata* Hagen, *A. straminea* Hagen, *Beothukus complicatus* (Banks), and *Fabria inornata* (Banks). One exception to the dominance of lentiphilic species was that of the rheophilic *Cheumatopsyche analis* (Banks) (Hydropsychidae) in First Lake (Table 2). This site was ~65 m upstream and in view of the outflow of the lake; thus, the *C. analis* specimens probably emerged from that natal habitat.

The taxonomic distinctiveness of the 2 vernal pools was particularly notable. Both pools had obvious standing water from May–June 2022, but none from July–October. Nonetheless, adult caddisflies were collected at both habitats throughout the entire sampling period. While it is possible that specimens flew to the vernal pools from a nearby permanent lake, several species, including summer and fall emergent limnephilid and phryganeid shredders, were found at a greater abundance near the vernal pool sites than at the permanent sites, suggesting that vernal pool species can either exist in very low water or else live for several months after adult emergence.

The lack of taxonomic separation between inland lake sites and those of Lake Huron, and the dominance of shredders in both habitat types, supports a lack of distinctiveness among types of Drummond Island lakes. Whereas riverine systems have had many models proposed to predict changes in benthic macroinvertebrate taxonomy or FFG ecology based on stream size and other factors (Vannote et al. 1980, Thorp et al. 2006, Maasri et al. 2021), lake environments have received less attention. Most proposed models assessing taxonomic or FFG differences between lakes have focused primarily on level of eutrophication rather than fundamental variables such as area, depth, bottom sub-

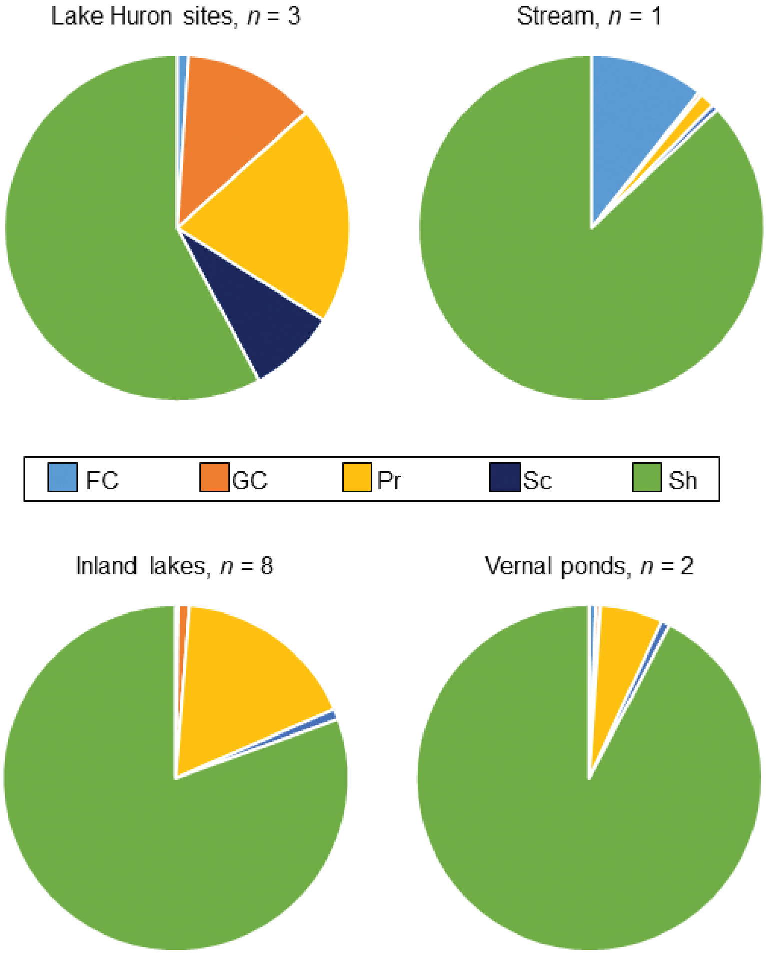

Figure 5. The relative AFDM biomass of 5 caddisfly FFGs within the 4 types of habitats sampled on Drummond Island, based on 1 summer (late June to mid-July) and 1 fall (early to mid-September) ultraviolet light sample for each site. FC = filtering collector, GC = gathering collector, Pr = predator, Sc = scraper, Sh = shredder. Algal piercers omitted due to composing <1% of the AFDM of each sample. No significant difference was found in mean AFDM of each FFG between inland lakes and Lake Huron sites based on nonparametric Mann-Whitney *U*-tests (FC: $p = 0.06$, GC: $p = 0.37$, Pr: $p = 0.54$, Sc: $p = 0.25$, Sh: $p = 0.27$). The stream and vernal pool habitats were not analyzed due to low sample size.

strate type, or level of shoreline vegetation (Pace et al. 2004, Galloway et al. 2014, Lau et al. 2014, Tanentzap et al. 2017). In a study of undisturbed Finish lakes, Heino (2008) found that benthic shredders increased in abundance with lake surface area, aquatic macrophytes, total phosphorous, and water hardness, but surprisingly not with that of percent shoreline coverage by deciduous trees. The high relative biomass of shredders in the undisturbed lakes of Drummond Island suggests that coarse allochthonous input is important to natural lake food webs just as it is for streams (Vannote et al. 1980, Houghton 2022). While only caddisflies were sampled in this study, trends in caddisfly FFG ecology usually reflect those of the overall aquatic macroinvertebrate assemblage (Dohet 2002, Houghton and Wasson 2013, Houghton et al. 2018b, Morse et al. 2019a, Houghton 2021a).

Drummond Island is the third area of northern Michigan to have both lakes and streams recently sampled for adult caddisflies from spring to fall with a rigorous effort. The 89 species reported herein compares to 169 from the Huron Mountains in the northern Upper Peninsula (Houghton 2022) and 114 from the Black River Ranch in the northern Lower Peninsula (Houghton 2016). Of the 89 species found on Drummond Island, 76 were also found in the Huron Mountains and 64 were also found at the Black River Ranch. The Black River Ranch yielded 51 species not found on Drummond Island and the Huron Mountains yielded 94 species. Both the non-asymptotic shape and the relatively high number of species represented by a single specimen support substantial additional undiscovered species in all three areas. Nonetheless, the species richness relative to sampling effort was clearly lowest on Drummond Island than in the other two areas. This lower caddisfly richness may be due to it being a small island (MacArthur and Wilson 2016). While Drummond Island is only 2–3 km from the Michigan mainland, such a distance may present a significant impediment to weak-flying caddisflies and other aquatic insects (Peterson et al. 1999, Sommerhäuser et al. 1999, Brakel et al. 2015). DeWalt and South (2015) hypothesized a similar explanation for the low species richness of caddisflies (46) on Lake Superior's Isle Royale, an island 25 km from mainland Minnesota and Ontario, in particular due to their weak flight and low vagility. It is also possible that the thin-soil environments and the lack of different stream sizes and morphologies may lead to naturally lower species richness on Drummond Island (Lincoln 2018).

Although no undescribed species or new state records were collected, there were some captures of unique or rarely collected species during this study (Table 3). *Beothukus complicatus* is known primarily from Canada, with very few specimens reported from Minnesota and Wisconsin (Rasmussen and Morse 2021). Houghton et al. (2018a) tentatively reported the species from Michigan based on unpublished reports without corresponding voucher specimens. The 6 specimens from 3 localities reported herein constitute the first confirmed presence of the species in the state, and doubles the number of known specimens from the entire United States (Longridge and Hilsenhoff 1972, Houghton 2012). With a single specimen from Potagannissing Bay in Lake Huron (site 3), *Holocentropus milaca* Etnier (Polycentropodidae) is now known worldwide from only 6 sites, all in Minnesota or Michigan (Houghton 2012, Houghton et al. 2018b). *Limnephilus parvulus* (Banks) (Limnephilidae), *F. inornata*, and *A. colorata* (Phryganeidae) are all species that have been previously reported from Michigan, but not within the last 50–70 years. Our specimens confirmed their extant presence in the state. *Glyphopsyche irrorata* (F.) (Limnephilidae) is a rarely collected species, as it emerges in late fall, overwinters as an adult, and dies out in April or May (Berté and Pritchard 1983). *Hydropsyche alternans* (Walker) (Hydropsychidae) was suggested by Miess et al. (2022) as possibly extirpated from the Great Lakes other than Lake Superior due to zebra mussel [*Dreissena polymorpha* (Pallas)] encroachment. Our specimens from Fairview Cove confirmed its adult presence at Lake Huron, nearly 100 km from Lake Superior.

Due to the proximity of sites to each other in this study, it is possible that some specimens that originated in one natal habitat were collected by a light trap of a different habitat. For example, the high abundance of the common rheophilic species *C. analis* in First Lake was likely due to the sampling site being within 65 m of and in view of the lake outflow. While this problem can never be completely eliminated, many studies have demonstrated that the low vagility of caddisflies promotes minimal specimen 'leakage' between sampling sites, especially sites that are not visible from each other (Sode and Wiberg-Larson 1993, Peterson et al. 1999, Sommerhäuser et al. 1999, Calor and Mariano 2012, Houghton and Wasson 2013, DeWalt and South 2015, Houghton et al. 2018b, Pereira et al. 2020). Brakel et al. (2015), in particular, found a forest and meadow site along a single Michigan stream that were separated by ~100 m had minimal overlap in their specific forest- and meadow-dwelling caddisfly assemblages when using simultaneous ultraviolet light sampling of adult specimens. All of our sampling sites were >100 m apart and not visible to each other. Moreover, because we analyzed our assemblages using abundance (Fig. 4) and ash-free dry mass (Fig. 5) data, the presence of an occasional errant specimen would have had minimal effects on our results, especially since errant specimens are usually of common and abundant species that are generally non-informative of habitat conditions (Peterson et al. 1999).

Some other potential experimental error may have been due to the challenges of sampling adult caddisflies representatively with blacklight traps. It is not known definitively if such traps are exhaustive, if they attract all species equally, or if species are less attracted at certain specific points during their adult flight period (Myers and Resh 1999, Nakano and Tanida 1999). Moreover, it is nearly impossible without electronic timers or a large field crew, to run each light for an identical period of time. Such inconsistencies could potentially have affected our results, particularly our biomass comparisons. Fortunately, the vast majority of both specimens and species in northern Michigan, including those of all FFGs, are caught in blacklight traps within the first 1–2 h after dusk (Wright et al. 2013, Brakel et al. 2015). Thus, any error in our study was probably minimal.

Since nearly 20% of the caddisfly species that we collected were represented by a single specimen (Fig. 3), it is likely that additional species remain to be discovered on Drummond Island. Such a situation likely occurs in areas throughout the north-central US and elsewhere. Thus, further research should include sampling caddisflies and other aquatic insects from unique and undisturbed habitats throughout the region. Further sampling of lake habitats is particularly important so that models can be generated to predict changes in aquatic insect assemblages relative to specific lake variables.

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