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The Caddisflies (Trichoptera) of Finch Creek, Antrim County, Michigan

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Abstract

The caddisfly assemblages of Finch Creek, a small woodland stream in northern Lower Michigan, were sampled along its entire continuum during May, June, July, and September 2021–2022 using ultraviolet blacklight traps. A total of 98 species representing 15 families and 49 genera were collected, including two species [*Lepidostoma prominens* (Banks) and *L. sommermanae* (Ross)] not previously reported from Michigan, and several others either not previously found in the Lower Peninsula or not reported from the state for >70 years. A non-metric multidimensional scaling ordination determined distinct species assemblages corresponding to the spring, summer, and fall months. Shredders dominated the assemblages of nearly all sites and seasons, with 60–90% of assemblage total organic biomass. Changes in caddisfly functional feeding group biomass approximated those predicted by the river continuum concept, except for an unexpected decrease in scrapers as the stream widened, possibly due to high sediment input into the creek. In addition to the new species records, this study further validated the use of caddisfly adults to assess aquatic ecosystems and demonstrated the dominance of shredders in small temperate woodland streams.

Keywords: Stream, assemblage, biomass, functional feeding group, season

Caddisfly research in Michigan has been ongoing for over 70 years (Leonard and Leonard 1949, Houghton et al. 2018), and the fauna of the state is one of the best known within the United States (Houghton et al. 2022). Despite these efforts, however, additional state records and undescribed species continue to be found in the state (DeWalt and South 2015, Houghton 2020, Houghton 2021b). Moreover, the gap in collecting effort that occurred between the 1950s and the 2000s means that many species have not been seen in decades and their continued presence in the state is not established. Thus, additional species and records almost certainly remain to be discovered or rediscovered in under-collected regions of Michigan.

Finch Creek is one of over 200 streams in the Elk River Chain of Lakes watershed, located in northwestern Lower Michigan (Silver et al. 2016) (Fig. 1). Because of the short length (< 7 km) and easy accessibility, Finch Creek is an ideal stream to sample along its entire continuum, from headwaters to mouth. The creek is one of the three main tributaries of Grass River, all of which pass through the 603 ha Grass River Natural Area (GRNA). Nine natural plant communities are found within the GRNA, with Finch Creek passing through primar-

ily mesic northern forest at its headwaters, then hardwood-conifer swamp and northern wet meadow, and finally northern fen as it flows northward to Grass River (Hackett et al. 2017). The GRNA staff welcomes natural inventory research, and the area was recently the site of a comprehensive beetle survey (Haack and Ruesink 2020, GRNA 2023).

The primary purpose of our study was to conduct a species inventory of caddisflies through multiple seasons along the entire continuum of Finch Creek and including sites within the GRNA. We predicted that our thorough sampling of this stream would find new state records or other unique species. A secondary purpose was to analyze differences in caddisfly assemblages and organic biomass between sites and seasons.

Materials and Methods

We selected five sites along Finch Creek (Figs. 1, 2). Sites were chosen to encompass the entire continuum of the creek as well as those having reasonable road or trail access. They ranged from the 1st order headwaters to the 3rd order confluence with Grass River (Table 1). Due to access difficulties, the latter site was about 15 m from the actual mouth of Finch Creek (Fig. 2E). Sites

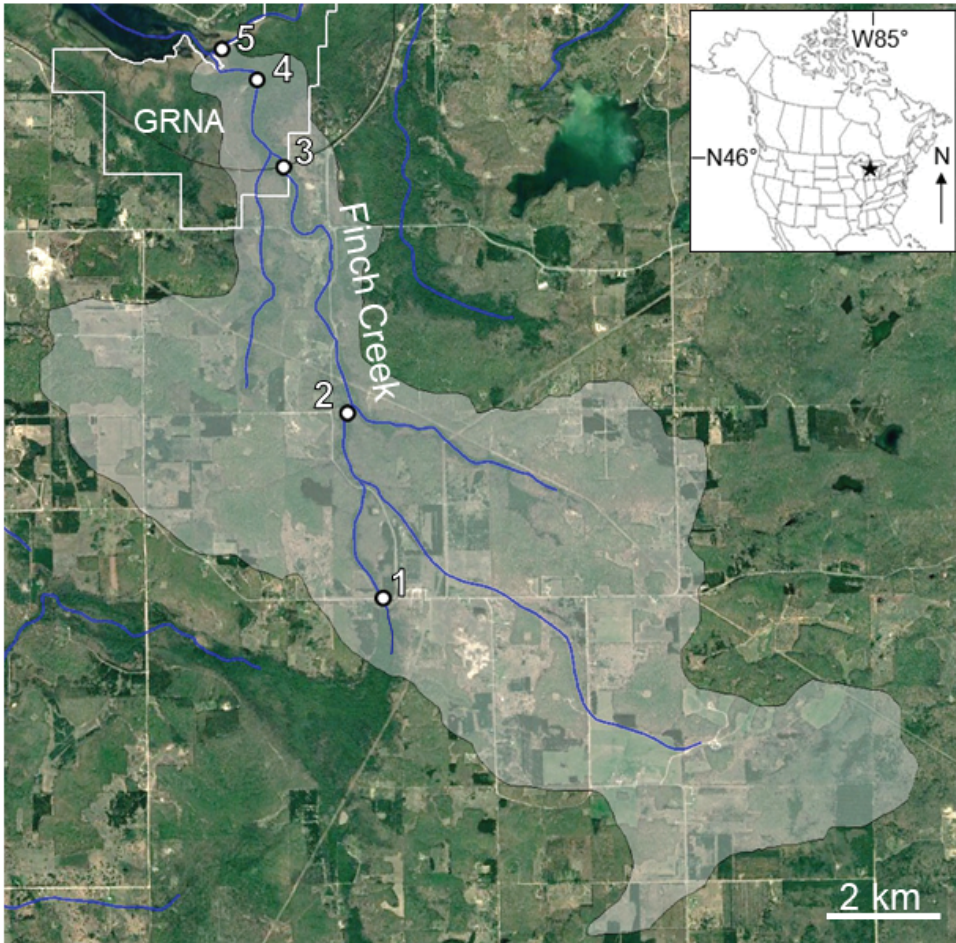


Figure 1. Map of our study area showing the approximate boundaries of the Finch Creek watershed and the Grass River Natural Area (GRNA). Watershed and stream boundaries based on the US EPA StreamCat database (<https://watersgeo.epa.gov/watershedreport>). Site numbers 1-5 correspond to Table 1. Base map © Google, TerraMetrics.

1-2 were upstream of the GRNA and sites 3-5 were within the preserve. Upstream land was a mixture of public and private ownership for all sites, with intact upstream habitat ranging from 75-85% (Table 1).

All five sites were sampled on 19 June, 10 July, and 09 September 2021, and on 12 May and 20 June 2022. The exception was Site 2 (Elder Road) which was not sampled in June 2021. Thus, we collected 24 total samples.

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. Traps were placed within 2 m of the shoreline either directly on the ground, slightly

(~50 cm) elevated above the surrounding vegetation if necessary, or on a nearby dock if available. In June and July, lights were turned on before dusk and collected 90-150 minutes after dusk. In May and September, lights were collected 120-180 minutes after dusk. Traps were always set out in site 1-5 order and picked up in 5-1 order. May-July samples were collected only if the peak daytime temperature was >24 °C, dusk temperature was >21 °C, and there was minimal wind and no precipitation at dusk (Houghton 2004). During the cooler month of September, samples were collected when the daytime high was >20 °C and dusk was >17 °C. Since aquatic insects collected within 100 m of a habitat accurately reflect the assemblage of that habitat (Peterson et al.



Figure 2. The five Finch Creek sampling sites of our study: Site 1 = Bebb Road (A), Site 2 = Elder Road (B), Site 3 = Rail Trail (C), Site 4 = Old Cabin (D), Site 5 = confluence of Finch Creek with Grass River (E).

Table 1. The five sites along Finch Creek sampled during this study. Site numbers correspond to Fig. 1. Stream order based on Strahler (1957). Habitat: the percentage of upstream habitat classified as forest, wetland, or grassland based on the USEPA Stream-Cat database (<https://watersgeo.epa.gov/watershedreport>), accessed 03 January 2023 (Hill et al. 2016).

#	Site name	Latitude	Longitude	Elevation (m)	Order	Habitat
1	Bebb Road	44.8739	-85.2056	240	1	85.7%
2	Elder Road	44.8883	-85.2092	213	2	84.0%
3	Rail Trail	44.9078	-85.2158	188	2	85.5%
4	Old Cabin	44.9147	-85.2186	185	2	85.9%
5	Grass River	44.9172	-85.2225	178	3	74.5%

Table 2. Ash-free dry mass (AFDM) and functional feeding group (FFG) affinity coding data for the 49 caddisfly genera collected from Finch Creek during this study. 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. (2019) and Houghton (2021a). FC = filtering collector, GC = gathering collector, Pr = predator, Sc = scraper, Sh = shredder. Algal piercing was considered a subset of gathering collector. Codes = '0' for no affinity for a FFG, '1' for low affinity, '2' for moderate affinity, '3' for high affinity, and '4' for near exclusive affinity.

Genus	AFDM (mg)	FFG affinity codes				
		FC	GC	Pr	Sc	Sh
<i>Agraylea</i>	0.029	0	4	0	0	0
<i>Agrypnia</i>	3.059	0	0	0	0	4
<i>Anabolia</i>	2.413	0	1	0	0	3
<i>Asynarchus*</i>	2.413	0	1	0	0	3
<i>Banksiola</i>	1.371	0	0	1	0	3
<i>Brachycentrus</i>	0.745	3	0	0	0	1
<i>Ceraclea</i>	0.695	0	2	1	0	1
<i>Cheumatopsyche</i>	0.346	4	0	0	0	0
<i>Chimarra</i>	0.402	4	0	0	0	0
<i>Dolophilodes*</i>	0.402	4	0	0	0	0
<i>Glossosoma</i>	0.284	0	0	0	4	0
<i>Glyphopsyche*</i>	2.413			unknown		
<i>Hagenella*</i>	3.059			unknown		
<i>Helicopsyche</i>	0.223	0	0	0	4	0
<i>Hesperophylax*</i>	3.973	0	1	0	0	3
<i>Holocentropus*</i>	0.418	1	0	3	0	0
<i>Hydatophylax</i>	6.521	0	1	0	0	3
<i>Hydropsyche</i>	0.392	4	0	0	0	0
<i>Hydroptila</i>	0.017	0	3	0	1	0
<i>Lepidostoma</i>	0.469	0	1	0	0	3
<i>Leptocerus</i>	0.235	0	1	0	0	3
<i>Limnephilus</i>	1.549	0	1	0	0	3
<i>Micrasema</i>	0.094	1	1	0	0	2
<i>Lype*</i>	0.038	0	2	0	2	0
<i>Molanna</i>	0.715	0	1	1	2	0
<i>Mystacides</i>	0.321	0	3	0	0	1
<i>Nectopsyche</i>	0.594	0	1	1	0	2
<i>Nemotaulius</i>	5.515	0	0	0	0	4
<i>Neophylax</i>	0.329	0	0	0	4	0
<i>Neureclipsis</i>	0.320	2	0	1	0	1
<i>Nyctiophylax</i>	0.105	1	0	2	0	1
<i>Oecetis</i>	0.452	0	0	3	0	1
<i>Onocosmoecus*</i>	2.199	0	0	0	0	4
<i>Orthotrichia</i>	0.011	0	4	0	0	0
<i>Oxyethira*</i>	0.011	0	4	0	0	0
<i>Parapsyche</i>	0.472	3	0	0	0	1
<i>Phryganea</i>	6.846	0	0	1	0	3
<i>Platycentropus</i>	3.973	0	0	0	0	4
<i>Plectrocnemia*</i>	0.418	1	0	3	0	0
<i>Polycentropus</i>	0.418	1	0	3	0	0
<i>Pseudostenophylax</i>	1.995	0	1	0	0	3
<i>Psychoglypha*</i>	1.549			unknown		
<i>Psychomyia</i>	0.038	0	3	0	1	0
<i>Ptilostomis</i>	7.217	0	0	1	0	3
<i>Pycnopsyche</i>	2.199	0	0	0	1	3
<i>Rhyacophila</i>	1.402	0	1	1	0	0
<i>Setodes</i>	0.192	0	3	1	0	0
<i>Triaenodes</i>	0.595	0	1	0	0	3
<i>Wormaldia*</i>	0.402	4	0	0	0	0

1999, Brakel et al. 2015), dispersals of adults between sites, while certainly possible, were considered unimportant.

Specimens were identified to species using Houghton's (2012) treatment of the Minnesota caddisflies or with more specific taxonomic treatments as needed. Identified specimens were coded with their affinity for one of five different functional feeding groups (FFGs) based on Morse et al. (2019) and Houghton (2021a): filtering collectors, gathering collectors, predators, scrapers, and shredders (Table 2). Algal piercing was considered a subset of gathering collector. Codes for each species consisted of '0' for no affinity for a FFG, '1' for low affinity, '2' for moderate affinity, '3' for high affinity, and '4' for near exclusive affinity (Chevenet et al. 1994, Houghton 2021a). 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 were estimated based on Houghton and Lardner (2020) (Table 2). All species within a genus were assigned the same value. Genera without a determined value were assigned the value of a genus of similar body size. 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 (Wagner 2002, 2005; Houghton and Lardner 2020), 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).

To delineate differences between caddisfly assemblages of different stream sites and months, specimens of the 24 samples were examined with a non-metric multidimensional scaling (NMDS) ordination using the program PC-ORD v.7 for Windows (Peck 2016). 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 determined NMDS axis in the calculated distance matrix. Samples were grouped into determined seasons and the mean AFDM between them was assessed with non-parametric Kruskal-Wallis tests using the Real Statistics add-in for Excel (www.real-statistics.com).

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>). In addition to the basic curve, two estimators were calculated to predict the actual species richness of our sampling area. The abundance-based coverage estimator (ACE) predicts total species richness based on a proportion of rare species to common species, defining 'rare' as any species represented by <10 specimens. The incidence-based coverage estimator (ICE) makes the same prediction, but defines 'rare' as any species found in <10 samples.

To assess changes in assemblage biomass along our continuum of five sites, simple linear regression models were calculated for the mean biomass per site for each of the five FFGs separately (dependent variable) based on the accumulated distance from the headwaters of Finch Creek (independent variable). A model was also calculated for mean total biomass of each site. Distance from headwaters was determined by using the 'Ruler' feature in Google Earth and measuring the accumulated stream distance from the first discernable channel (Fig. 1).

Results

Based on identification of 2380 specimens, we report 98 caddisfly species representing 15 families and 49 genera (Table 3). *Oecetis inconspicua* (Walker) (Leptoceridae) was the most abundant species, followed by *Agraylea multipunctata* Curtis (Hydroptilidae) and *Brachycentrus americanus* (Banks) (Brachycentridae). Over a quarter (26 of 98) of species were represented by a single specimen. The family Leptoceridae had the most species (19), followed by Limnephilidae (18) and Hydroptilidae (12). Total richness ranged from 36–60 species per site, with the two most downstream sites collectively containing 27 of the 32 species found only at a single site. Each month contained species found only during that particular month. Both estimators predicted that another 20–25 species still remain to be found from our sampling sites (Fig. 3).

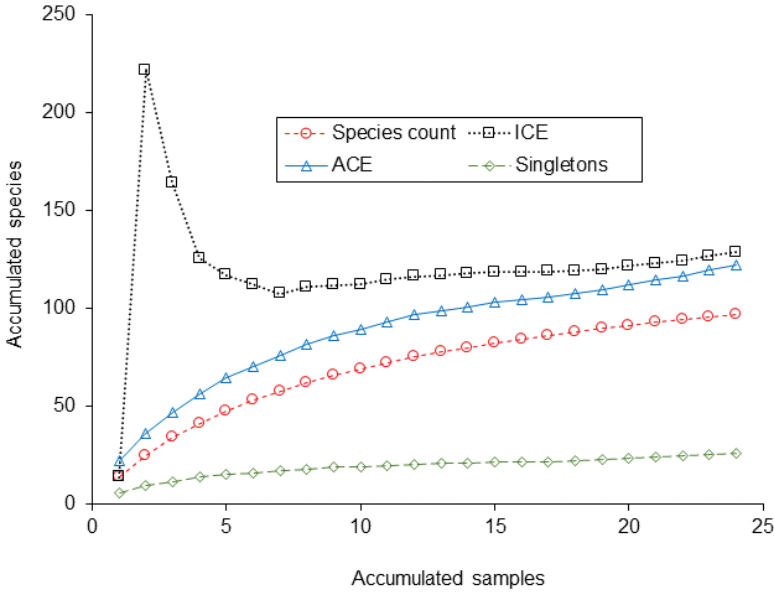


Figure 3. Species accumulation curve for our 24 samples, showing the accumulated number of species, the number of species represented by a single specimen (singletons), and two estimators: the abundance-based coverage estimator (ACE) and the incidence-based coverage estimator (ICE) of actual species richness. For each series, 100 randomized combinations of sample order were calculated and then a mean value determined and displayed.

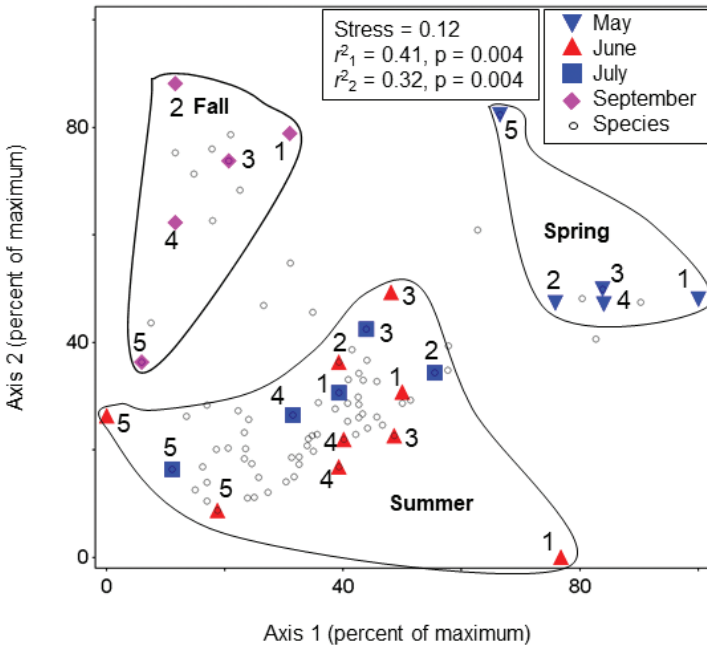


Figure 4. Non-metric multidimensional scaling ordination of our 24 samples based on caddisfly \log_{10} abundance per species per sample and grouped per month. *P*-values from a Monte Carlo test of non-random ordination structure. Site numbers correspond to Table 1 and Figure 1. Species labels omitted for clarity.

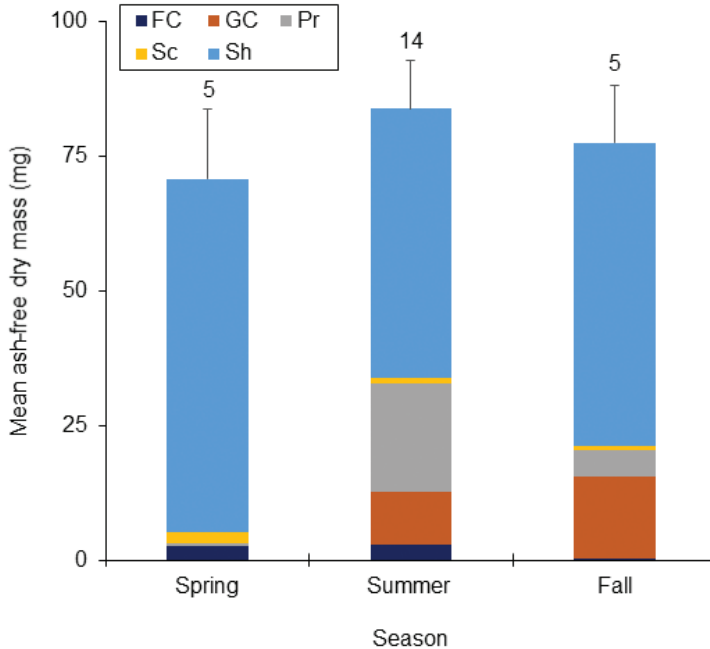


Figure 5. Mean (+SE) ash-free dry mass per functional feeding group (FFG) per collecting site for our five sites. Sample sizes above each bar. FFGs: FC = filtering collectors, GC = gathering collectors, Pr = predators, Sc = scrapers, Sh = shredders. No significant difference was found in the mean AFDM of each FFG between the seasons based on nonparametric Kruskal-Wallis tests, except for predators which were highest in the summer and gathering collectors which were lowest in the spring (Total: $p = 0.42$, FC: $p = 0.85$, GC: $p = 0.04$, Pr: $p = <0.001$, Sc: $p = 0.80$, Sh: $p = 0.18$).

An NMDS ordination of all 24 samples produced a two-dimensional solution explaining 73% of the variation in the data set (Fig. 4). May and September assemblages were distinct from each other and from June and July assemblages, which were not distinct from each other. Thus, June and July assemblages were grouped together into ‘Summer’, whereas May and September remained ‘Spring’ and ‘Fall’, respectively. Although differences in assemblages were more distinct between months than between sampling sites, assemblages of the Grass River (site 5) were generally similar to each other and distinct from those of other sites.

Mean total and per FFG caddisfly biomass per sample were similar for all three seasons, except for predators being highest during the summer and gathering collectors lowest in the spring (Fig. 5). Shredders composed 60–90% of all seasonal assemblages. Individually, *Hesperophylax designatus* (Walker) (Limnephilidae) had the highest biomass among species, followed by *Banksiola crotchii* (Banks) (Phryganeidae),

and *Brachycentrus americanus* (Table 3). Collectively, the top six species represented over half of the biomass of the total caddisfly assemblage.

Models predicting total biomass and that of the individual FFGs based on distance from the headwaters all had R^2 values of 0.23–0.86, and were mostly non-significant when using a standard alpha value of 0.05 (Fig. 6). Total biomass, plus that of filtering collectors, gathering collectors, and predators all increased non-significantly along the continuum, whereas biomass of shredders decreased. Scraper biomass decreased significantly along the continuum.

Discussion

This study demonstrated the necessity of sampling multiple sites to capture maximal species richness, even within a relatively small area and along the same stream. Caddisflies are weak flyers with low vagility, thus documenting the species of particular habitats requires sampling close to each

Table 3. Summary data for the 98 species of Trichoptera collected during this study, including the total number of specimens found at each of the five sites, the mean number of specimens per sample found during each of the four months, and the total biomass for each species. Site numbers correspond to Table 1 and Figure 1. Taxa are arranged alphabetically by family and genus. Number of species within each family in parentheses. New state records for Michigan in boldface font. Total biomass was determined by multiplying the total number of specimens of each species by its AFDM value in Table 2.

Taxon	Total specimens per site					Mean specimens per month				Total biomass	
	1	2	3	4	5	Total	May	June	July		Sep
BRACHYCENTRIDAE (3)											
<i>Brachycentrus americanus</i> (Banks) 1899	0	1	124	61	2	188	0.2	3.3	3.0	28.4	140.1
<i>Micrasema rusticum</i> (Hagen) 1868	0	0	0	1	0	1	0.0	0.0	0.2	0.0	0.1
<i>Micrasema wataga</i> Ross 1938	0	0	0	1	0	1	0.0	0.0	0.2	0.0	0.1
GLOSSOSOMATIDAE (2)											
<i>Glossosoma intermedium</i> (Klapálek) 1892	37	1	0	0	0	38	6.6	0.6	0.0	0.0	10.8
<i>Glossosoma nigrior</i> Banks 1911	10	7	0	0	0	17	0.0	1.1	1.4	0.0	4.8
HELICOPSYCHIDAE (1)											
<i>Helicopsyche borealis</i> (Hagen) 1861	0	1	2	1	0	4	0.0	0.4	0.0	0.0	0.9
HYDROPSYCHIDAE (6)											
<i>Cheumatopsyche analis</i> (Banks) 1908	4	1	6	6	0	17	0.0	1.7	0.4	0.0	5.9
<i>Cheumatopsyche campyla</i> Ross 1938	2	0	0	12	10	24	0.0	2.3	0.6	0.0	8.3
<i>Diplectrona modesta</i> Banks 1908	0	0	0	1	0	1	0.0	0.0	0.2	0.0	0.4
<i>Hydropsyche slossonae</i> Banks 1905	0	0	0	1	0	1	0.0	0.1	0.0	0.0	0.4
<i>Hydropsyche sparna</i> Ross 1938	7	1	1	0	0	9	0.0	0.7	0.4	0.2	3.5
<i>Parapsyche apicalis</i> (Banks) 1908	9	41	18	13	0	81	6.8	4.2	1.8	0.0	31.8
HYDROPTILIDAE (12)											
<i>Agraylea multipunctata</i> Curtis 1834	3	0	1	3	248	255	0.0	18.2	9.2	9.0	7.4
<i>Hydroptila ampoda</i> Ross 1941	0	0	0	0	2	2	0.0	0.0	0.0	0.4	0.0
<i>Hydroptila armata</i> Ross 1938	0	1	0	11	75	87	0.0	5.9	1.4	5.4	1.5
<i>Hydroptila consimilis</i> Morton 1905	1	0	1	2	0	4	0.0	0.0	0.6	0.2	0.1
<i>Hydroptila waubesiana</i> Betten 1934	0	0	0	3	6	9	0.0	1.0	0.0	0.0	0.2
<i>Hydroptila xera</i> Ross 1938	0	0	0	1	0	1	0.0	0.0	0.2	0.0	0.0
<i>Orthotrichia cristata</i> Morton 1905	0	0	0	0	1	1	0.0	0.1	0.0	0.0	0.0
<i>Oxyethira coerens</i> Morton 1905	1	0	0	0	31	32	0.0	3.6	0.0	0.0	0.4
<i>Oxyethira forcipata</i> Mosely 1934	0	0	0	0	1	1	0.0	0.0	0.0	0.2	0.0

<i>Oxyethira obtatus</i> Denning 1947	0	0	0	0	1	1	0.0	0.1	0.0	0.0	0.0	0.0
<i>Oxyethira pallida</i> (Banks) 1904	0	0	0	0	1	1	0.0	0.1	0.0	0.0	0.0	0.0
<i>Oxyethira verna</i> Ross 1938	0	0	0	0	1	1	0.0	0.1	0.0	0.0	0.0	0.0
LEPIDOSTOMATIDAE (8)												
<i>Lepidostoma bryanti</i> (Banks) 1908	8	82	11	42	0	143	0.0	9.1	12.2	0.0	67.1	0.0
<i>Lepidostoma cinereum</i> (Banks) 1899	0	0	0	0	1	1	0.0	0.0	0.0	0.2	0.5	0.0
<i>Lepidostoma costale</i> (Banks) 1914	0	2	0	2	0	4	0.0	0.0	0.0	0.8	1.9	0.0
<i>Lepidostoma griseum</i> (Banks) 1911	1	1	3	0	0	5	0.0	0.0	0.0	1.0	2.3	0.0
<i>Lepidostoma prominens</i> (Banks) 1930	5	9	4	8	0	26	0.0	0.0	0.0	5.2	12.2	0.0
<i>Lepidostoma sommermanae</i> Ross 1938	1	0	0	0	0	1	0.0	0.1	0.0	0.0	0.5	0.0
<i>Lepidostoma togatum</i> (Hagen) 1861	0	0	1	0	0	1	0.2	0.0	0.0	0.0	0.5	0.0
<i>Lepidostoma vernale</i> (Banks) 1897	3	0	0	0	0	3	0.0	0.3	0.0	0.0	1.4	0.0
LEPTOCERIDAE (19)												
<i>Ceraclea alagma</i> (Ross) 1938	1	0	0	1	21	23	0.0	0.0	4.6	0.0	16.0	0.0
<i>Ceraclea arielles</i> (Denning) 1942	0	0	1	0	0	1	0.0	0.0	0.2	0.0	0.7	0.0
<i>Ceraclea cancellata</i> (Betten) 1934	0	0	0	0	9	9	0.0	0.9	0.2	0.0	6.3	0.0
<i>Ceraclea diluta</i> (Hagen) 1861	0	0	0	0	2	2	0.0	0.2	0.0	0.0	1.4	0.0
<i>Ceraclea maculata</i> (Banks) 1899	0	0	1	0	0	1	0.0	0.0	0.2	0.0	0.7	0.0
<i>Ceraclea resurgens</i> (Walker) 1852	0	0	0	0	7	7	0.0	0.8	0.0	0.0	4.9	0.0
<i>Ceraclea tarsipunctata</i> (Vorhies) 1909	0	0	2	0	5	7	0.0	0.1	1.2	0.0	4.9	0.0
<i>Ceraclea transversa</i> (Hagen) 1861	0	0	0	3	116	119	0.0	0.3	23.2	0.0	82.7	0.0
<i>Leptocerus americanus</i> (Banks) 1899	1	0	0	5	35	41	0.0	0.1	8.0	0.0	9.6	0.0
<i>Mystacides interjectus</i> (Banks) 1914	0	0	1	2	2	5	0.0	0.6	0.0	0.0	1.6	0.0
<i>Mystacides sepulchralis</i> (Walker) 1852	0	0	0	3	9	12	0.0	1.1	0.4	0.0	3.9	0.0
<i>Oecetis cinerascens</i> (Hagen) 1861	2	1	0	2	12	17	0.0	1.8	0.2	0.0	7.7	0.0
<i>Oecetis inconspicua</i> (Walker) 1852	45	7	40	52	142	286	0.0	29.3	4.2	0.2	129.3	0.0
<i>Oecetis osteni</i> Milne 1934	1	0	1	0	2	4	0.0	0.3	0.2	0.0	1.8	0.0
<i>Oecetis persimilis</i> (Banks) 1907	0	0	0	1	4	5	0.0	0.6	0.0	0.0	2.3	0.0
<i>Setodes oligius</i> (Ross) 1938	0	0	0	0	17	17	0.0	1.9	0.0	0.0	3.3	0.0
<i>Trienodes injustus</i> (Hagen) 1861	1	0	30	14	43	88	0.0	6.9	3.8	1.4	52.4	0.0
<i>Trienodes marginatus</i> Sibley 1926	1	0	3	16	34	54	0.0	2.7	2.6	3.4	32.1	0.0
<i>Trienodes tardus</i> Milne 1934	0	0	3	7	24	34	0.0	3.2	1.0	0.0	20.2	0.0

(Continued on next page)

Table 3. (Continued).

Taxon	Total specimens per site					Total	Mean specimens per month				Total biomass	
	1	2	3	4	5		May	June	July	Sep		
LIMNEPHILIDAE (18)												
<i>Anabolia bimaculata</i> (Walker) 1852	0	0	0	0	3	3	0.0	0.0	0.6	0.0	0.0	7.2
<i>Asynarchus montanus</i> (Banks) 1907	1	2	0	1	0	4	0.0	0.4	0.0	0.0	0.0	9.7
<i>Glyphosyche irrorata</i> (F.) 1781	1	0	0	2	0	3	0.6	0.0	0.0	0.0	0.0	7.2
<i>Hesperophylax designatus</i> (Walker) 1852	53	15	5	6	1	80	15.4	0.3	0.0	0.0	0.0	317.8
<i>Hydatophylax argus</i> (Harris) 1869	0	2	7	2	0	11	0.0	1.2	0.0	0.0	0.0	71.7
<i>Limnephilus externus</i> Hagen 1861	0	0	0	0	1	1	0.0	0.0	0.0	0.0	0.2	1.5
<i>Limnephilus moestus</i> Banks 1908	0	0	1	9	0	10	0.0	1.1	0.0	0.0	0.0	15.5
<i>Limnephilus ornatus</i> Banks 1897	2	1	0	1	0	4	0.0	0.2	0.4	0.0	0.0	6.2
<i>Limnephilus parvulus</i> (Banks) 1905	0	0	0	0	2	2	0.4	0.0	0.0	0.0	0.0	3.1
<i>Limnephilus submonilifer</i> Walker 1852	3	3	0	1	0	7	0.8	0.0	0.0	0.0	0.6	10.8
<i>Onocosmoecus unicolor</i> (Banks) 1897	0	7	25	7	1	40	0.0	0.0	0.0	0.0	8.0	88.0
<i>Platycentropus radiatus</i> (Say) 1824	0	0	0	1	0	1	0.0	0.1	0.0	0.0	0.0	4.0
<i>Pseudostenophylax sparsus</i> (Banks) 1908	0	3	1	0	0	4	0.2	0.2	0.2	0.0	0.0	9.7
<i>Psychoglypha subborealis</i> (Banks) 1924	0	1	0	0	0	1	0.2	0.0	0.0	0.0	0.0	2.2
<i>Pycnopsyche antica</i> (Walker) 1852	6	0	4	9	0	19	0.0	0.0	2.2	1.6	0.0	41.8
<i>Pycnopsyche circularis</i> (Provancher) 1877	0	0	1	0	0	1	0.0	0.0	0.0	0.2	0.0	2.2
<i>Pycnopsyche guttifer</i> (Walker) 1852	2	0	13	0	5	20	0.0	0.0	0.0	4.0	4.0	44.0
<i>Pycnopsyche lepida</i> (Hagen) 1861	0	0	0	1	5	6	0.0	0.0	0.0	1.2	1.2	13.2
MOLANNIDAE (2)												
<i>Molanna blanda</i> Sibley 1926	2	4	0	0	0	6	0.0	0.4	0.4	0.0	0.0	4.3
<i>Molanna uniophila</i> Vorhies 1909	0	0	0	0	4	4	0.0	0.2	0.4	0.0	0.0	2.9
PHILOPOTAMIDAE (3)												
<i>Chimarra obscura</i> (Walker) 1852	0	1	0	1	8	10	0.0	0.3	1.4	0.0	0.0	4.0
<i>Dolophilodes distinctus</i> (Walker) 1852	0	1	0	0	0	1	0.0	0.0	0.2	0.0	0.0	0.4
<i>Wormaldia moesta</i> (Banks) 1914	0	0	0	1	0	1	0.0	0.0	0.2	0.0	0.0	0.4
PHRYGANEIDAE (8)												
<i>Agrypnia improba</i> (Hagen) 1873	3	1	0	1	0	5	0.0	0.1	0.8	0.0	0.0	15.3
<i>Agrypnia vestita</i> (Walker) 1852	0	0	0	0	1	1	0.0	0.1	0.0	0.0	0.0	3.1
<i>Banksiola crotchii</i> Banks 1943	7	4	31	54	22	118	0.0	10.2	5.2	0.0	0.0	161.8
<i>Banksiola dossuaria</i> (Banks) 1907	5	0	0	8	0	13	0.0	1.4	0.0	0.0	0.0	17.8
<i>Hagenella canadensis</i> (Banks) 1907	1	0	0	0	0	1	0.0	0.0	0.2	0.0	0.0	3.1
<i>Phryganea cinerea</i> Walker 1852	3	0	0	2	0	5	0.0	0.0	1.0	0.0	0.0	34.2

<i>Ptilostomis ocellifera</i> (Walker) 1852	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.0	7.2
<i>Ptilostomis semifasciata</i> (Say) 1828	0	1	4	9	4	18	18	0	0	0	0	0	0	0	0	0	0	0.8	0.0	129.9
POLYCENTROPODIDAE (10)																				
<i>Holocentropus flavus</i> (Banks) 1908	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0.2	0.0	0.4
<i>Holocentropus interruptus</i> (Banks) 1914	1	1	3	0	4	9	9	0	0	0	0	0	0	0	0	0	0	0.2	0.0	3.8
<i>Neureclipsis crepuscularis</i> (Walker) 1852	0	0	0	1	27	28	28	0	0	0	0	0	0	0	0	0	0	2.6	0.0	5.5
<i>Nyctiophylax moestus</i> Banks 1911	1	0	0	0	2	3	3	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.3
<i>Plectrocnemia cinerea</i> (Hagen) 1861	2	0	0	1	82	85	85	0	0	0	0	0	0	0	0	0	0	10.4	3.6	35.5
<i>Plectrocnemia clinei</i> (Milne) 1936	1	2	2	11	0	16	16	0	0	0	0	0	0	0	0	0	0	1.0	0.0	6.7
<i>Plectrocnemia crassicornis</i> (Walker) 1852	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.4
<i>Plectrocnemia remota</i> Banks 1911	0	1	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0.2	0.0	0.8
<i>Polycentropus pentus</i> Ross 1941	3	4	7	16	0	30	30	0	0	0	0	0	0	0	0	0	0	1.4	0.0	12.5
<i>Polycentropus weedi</i> Blicke & Morse 1955	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.4
PSYCHOMYIIDAE (2)																				
<i>Lype diversa</i> (Banks) 1914	4	5	11	12	2	34	34	0	0	0	0	0	0	0	0	0	0	0.2	0.0	1.3
<i>Psychomyia flavida</i> Hagen 1861	0	0	0	6	1	7	7	0	0	0	0	0	0	0	0	0	0	0.2	0.0	0.3
RHYACOPHILIDAE (3)																				
<i>Rhyacophila brunnea</i> Banks 1911	4	4	12	7	0	27	27	0	0	0	0	0	0	0	0	0	0	1.2	1.2	37.9
<i>Rhyacophila manistee</i> Ross 1938	0	0	2	29	0	31	31	0	0	0	0	0	0	0	0	0	0	0.6	0.0	43.5
<i>Rhyacophila vibox</i> Milne 1936	0	3	1	2	0	6	6	0	0	0	0	0	0	0	0	0	0	0.0	0.0	8.4
THREMMATIDAE (1)																				
<i>Neophylax concinnus</i> MacLachlan 1871	0	4	0	1	0	5	5	0	0	0	0	0	0	0	0	0	0	0.2	0.8	1.6
Total specimens	249	226	384	481	1040	2380	2380	0	0	0	0	0	0	0	0	0	0	55	24	
Total species	41	36	37	60	49	98	98	11	65	25	24	11	4	4	4	4	4	14	11	
Total unique species	1	1	3	9	19	19	19	4	25	11	11	4	4	4	4	4	4	14	11	

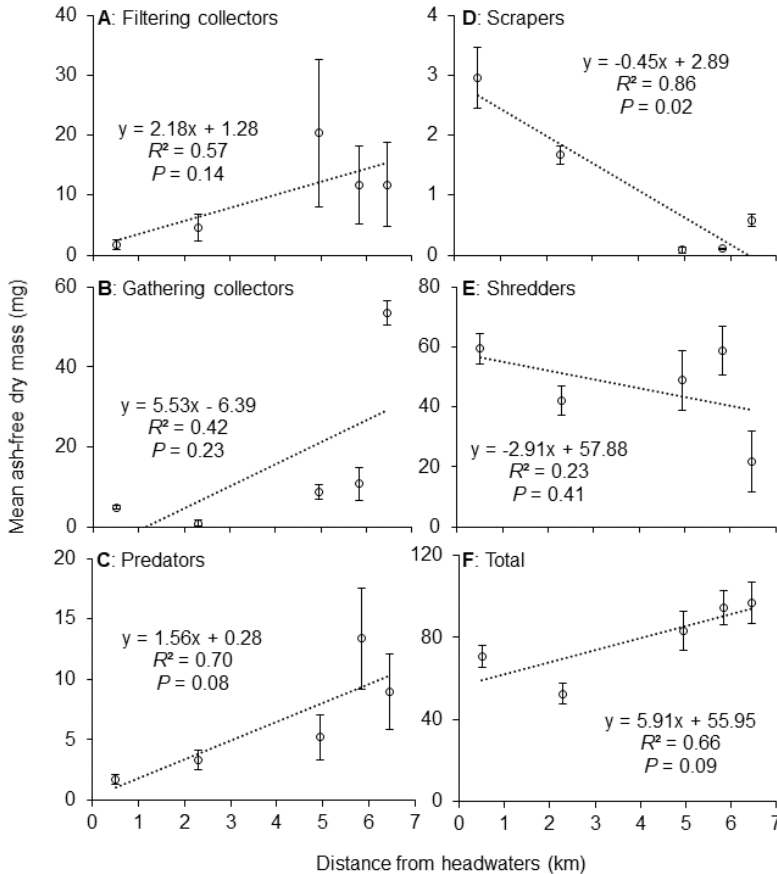


Figure 6. Simple linear regression models of mean (\pm SE) biomass per sampling site for filtering collectors (A), gathering collectors (B), predators (C), scrapers (D), and shredders (E) separately, and in sum total (F), based on distance from the Finch Creek headwaters.

habitat (Peterson et al. 1999, Brakel et al. 2015). Considering that >33% of all species were exclusive to a particular site, sampling only one or two sites of Finch Creek instead of five would have missed much of the fauna.

This study also demonstrated the importance of sampling throughout multiple seasons, as >50% of species were exclusive to a particular season. Several studies have determined different caddisfly flight periods, approximately corresponding to spring, summer, and fall, with particular assemblages unique to each (Swegman et al. 1981, Singh et al. 1984, Dobrin and Giberson 2003, Houghton 2015). Fall- and spring-emergent species are almost certainly more abundant than typically reported, simply because fewer collectors are out during those seasons, and because spring and fall tend to have suboptimal weather for blacklighting. Sampling only during the summer months

of this study would have missed 15–20% of the fauna, including several unique and rarely-collected species.

Two species new to Michigan were discovered during this study, both in the genus *Lepidostoma* (Lepidostomatidae). *Lepidostoma sommermanae* Ross was previously known from the eastern US and Canada, including Indiana and Ohio (Rasmussen and Morse 2021). While its presence in Michigan is not surprising, it is probably nearing the western edge of its range in the state. *Lepidostoma prominens* (Banks) is a rarely collected species that ranges from Labrador to Minnesota, including other northern states such as Massachusetts and New Hampshire (Rasmussen and Morse 2021). Some of its reported rarity may derive from its fall emergence, as we collected 26 total specimens from four of our study sites, but only during September. A thorough sampling

of other small Michigan streams in the fall would probably find additional populations of this species. Interestingly, eight of the 12 known species of Michigan *Lepidostoma* have been found in Finch Creek, more than double the typical number of *Lepidostoma* congeners found in Michigan stream samples (DCH, unpublished data).

In addition to the two state records, there were several other unique species collected during this study. Our specimens of *Wormaldia moesta* (Banks) (Philopotamidae) and *Pycnopsyche circularis* (Provancher) (Limnephilidae) represented the first known collections of these species from Michigan's Lower Peninsula. The former species has been collected sporadically in Michigan's Upper Peninsula, typically from high velocity streams and waterfalls (DCH, unpublished data). The latter species is probably more widespread than reported, but rarely collected due to its fall emergence. *Limnephilus externus* Hagen (Limnephilidae) and *Psychoglypha subborealis* (Banks) (Limnephilidae) are both species previously collected from Michigan (Leonard and Leonard 1949), but not reported in the state in >70 years. Both emerge late in the fall, with the latter species often overwintering as an adult before dying off in the early spring (Ellis 1978).

Our data supported consistent biomass across the three emergence seasons for most FFGs, and is one of the first studies to address this topic. Michigan streams that are relatively small and undisturbed have previously been observed to be dominated by shredders during both summer and fall, the latter season almost completely due to species in the genus *Pycnopsyche* (Houghton 2018, 2021a). In addition to these same findings, our study also determined a spring emergence dominated by shredders, particularly *Hesperophylax designatus* (Walker). While this species is relatively common throughout the northcentral US (Houghton et al. 2022), we have never seen an emergence as abundant as the one from Finch Creek. As with fall-emergent species, spring-emergent species are poorly known relative to those of the summer, and considerable research is still needed on their assemblages.

The relatively high R^2 values and non-significant P -values of most of our models predicting caddisfly FFG biomass based on stream distance from headwaters suggested strong associations between variables that should be viewed with low confidence due to small ($n = 5$) sample sizes. Assuming that observed trends are real, then our data generally supported changes in FFG biomass as predicted by the river continuum concept (RCC) (Vannote et al. 1980, Doretto et al.

2020). The concept predicts an increase in overall organismal biomass as rivers widen, a decrease in relative shredder biomass as coarse allochthonous input from the forest canopy decreases in importance, an increase in relative gathering collector and filtering collector biomass as fine particulate organic matter accumulates downstream, and an increase in relative scraper biomass as sunlight more easily penetrates to rock surfaces and stimulates periphyton growth. Subsequent studies have also observed an increase in predator biomass as rivers widen (Houghton 2021a, Koster et al. 2022). A frequent question about the concept has been that of spatial scale and how much river distance is necessary to observe organismal changes (Thorp et al. 2006, Maasri et al. 2021). Our data suggested that predicted RCC changes in caddisfly FFGs can be observed over distances <10 km, at least within lotic systems with physicochemical parameters similar to Finch Creek.

The exception to RCC predictions was scrapers, which decreased significantly instead of the expected increase. While the reason for this unexpected result is not clear, it may be due to the known high (~400 tons per year) sediment load from dirt road crossings along Finch Creek, including a large spate due to heavy rain in August 2021 (Richards 2012, DeColibus et al. 2014, Silver et al. 2016, McWhirter 2021). Caddisfly scrapers that are predicted to be abundant in 2nd–3rd order temperate woodland streams, such as *Glossosoma intermedium* (Klapálek), *G. nigrior* Banks (Glossosomatidae), and, especially, *Helicopsyche borealis* (Hagen) (Helicopsychidae), were all quite rare below Site 2 (Table 3). All of these species need exposed rock surfaces on which to consume periphyton, thereby being sensitive to excess sedimentation (Wiggins 2004). While we did not directly measure such variables at our sites, we did anecdotally observe a noteworthy increase in fine sediment below Site 1 and a decrease of exposed rock and cobble below Site 3. Further research is needed to address this hypothesis directly.

A likely source of some experimental error in our study was in the specific location of Site 5. Finch Creek empties into Grass River through a wet fen habitat, rendering access and blacklight placement unrealistic. So, we instead sampled 15 m downstream of the confluence on an easily-accessed dock (Fig. 2E). Thus, the species and biomass values obtained from Site 5 represented a combination of Finch Creek and Grass River faunas. This error is also indicated by the large number of unique species found at Site 5 and in its distinctness from other sites (Table 3, Fig. 4). Nonetheless, the site was still

on the same continuum as the other sites, so we included it in RCC analyses.

Another potential source of error was 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 RCC biomass predictions. 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.

Ultimately, this study demonstrated the importance of continued aquatic insect sampling, even in states like Michigan that are relatively well known. Nearly two dozen additional caddisfly species have been found in Michigan since Houghton et al.'s (2018) recent statewide checklist of 295 species, and the presence of many others has been re-established after not being reported for 50–70 years. Even our multi-season sampling of multiple sites along Finch Creek is predicted to have only captured 80% of the stream's actual caddisfly fauna (Fig. 3). Similarly, there are probably additional species and unique records still to be found in Michigan.

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