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Discontinuity in the Insect Assemblages of a Northern Lower Michigan Stream

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Abstract

We assessed the physicochemical and biological continuity of a 2nd–4th order reach of the Little Manistee River in northern Lower Michigan. Contrary to typical woodland streams, the downstream sites of the river were covered with a dense riparian canopy, whereas the upstream sites were devoid of this canopy due to historical (≥10 ybp) agriculture. Other than slight changes in water temperature and dissolved oxygen, there were no appreciable differences in measured water physicochemistry between the canopied and non-canopied sites. The stream, however, appeared biologically discontinuous as indicated by lower shredder abundance and higher filtering collector abundance at the upstream (non-canopied) sites for both benthic macroinvertebrate and adult caddisfly assemblages. Benthic scraper abundance was, likewise, higher in the upstream sites. Our results suggest that changes in riparian canopy alone can lead to changes in biological assemblages, even without obvious changes in water physicochemistry.

The river continuum concept (Vannote et al. 1980) describes a predictable pattern of gradual changes in river morphometrics and organismal assemblages as width increases and the river interacts with its riparian corridor. Anthropogenic disturbances, however, may disrupt this continuum, particularly in small–medium streams (Pringle et al. 1993; Delong and Brusven 1993, 1998; Houghton 2006, 2007). Removal of the riparian canopy cover, for example, may cause a loss of coarse allochthonous input needed by invertebrate shredders (Sabater et al. 2000, Warren et al. 2007). Agricultural streams in particular have concentrations of sediment, nutrient, and fine organic matter input hundreds of times higher than undisturbed streams (Royer et al. 2004, Inwood at al. 2005). Riparian habitat loss, with subsequent increases in nutrient and sediment input, has been repeatedly found to be the most widespread stressor of streams in the U.S. generally, in the Plains and Lowlands region of the U.S., and in Michigan (Paulsen at al. 2008, Wang et al. 2008).

It is difficult to separate the habitat loss and sediment input components of riparian disturbance, as they frequently occur together. Several recent studies of agricultural watersheds, however, have noted positive correlations between the amount of intact riparian vegetation and the biological diversity in the adjacent streams (Houghton 2004a, Rios and Baily 2006, Urban et al. 2006). More specifically, Houghton et al. (2011a) found that sites in a southern Michigan agricultural stream protected by riparian canopy had 3× the number of adult caddisfly species as sites without canopy, even though physicochemistry remained unchanged and typical of agricultural streams. These studies suggest the hypothesis that both riparian habitat loss and increases in sediment

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input are individually important for affecting stream biota. The purpose of our study, therefore, was to test this hypothesis by observing the effects of riparian canopy loss on stream macroinvertebrate assemblages in a stream without obvious sediment input.

Materials and Methods

Study site. The Little Manistee River is located in the northwestern portion of the Lower Peninsula of Michigan. It is approximately 100 km in length and drains a watershed of approximately 1100 km^2 before draining into Lake Michigan. Over half of the watershed is officially protected by the Manistee National Forest and the Pere Marquette State Forest, and much of the remaining land is also undeveloped (Fig. 1). Due to its relatively undisturbed watershed and stable groundwater input, it is one of the coldest and most stable streams in the Lower Peninsula (Tonello 2005). It hosts potomadromous spawning runs of steelhead [*Oncorhynchus mykiss* (Walbaum)], Chinook salmon [*Oncorhynchus tshawytscha* (Walbaum)], and brown trout [*Salmo trutta* Linnaeus] from Lake Michigan, and contains breeding populations of brook trout [*Salvelinus fontinalis* (Mitchell)] (Seelbach 1993). Although much of the watershed is protected, the headwaters of the Little Manistee are primarily composed of pasture and feral fields (Tonello 2005). From our observations, it has been ~10 years since the upper watershed was under active cultivation.

Five sites were sampled on the Little Manistee during this study. Sites 1–2 were located in the non-canopied headwaters region and sites 3–5 were all within the forested State and National Forest land (Fig. 1). All 5 sites were

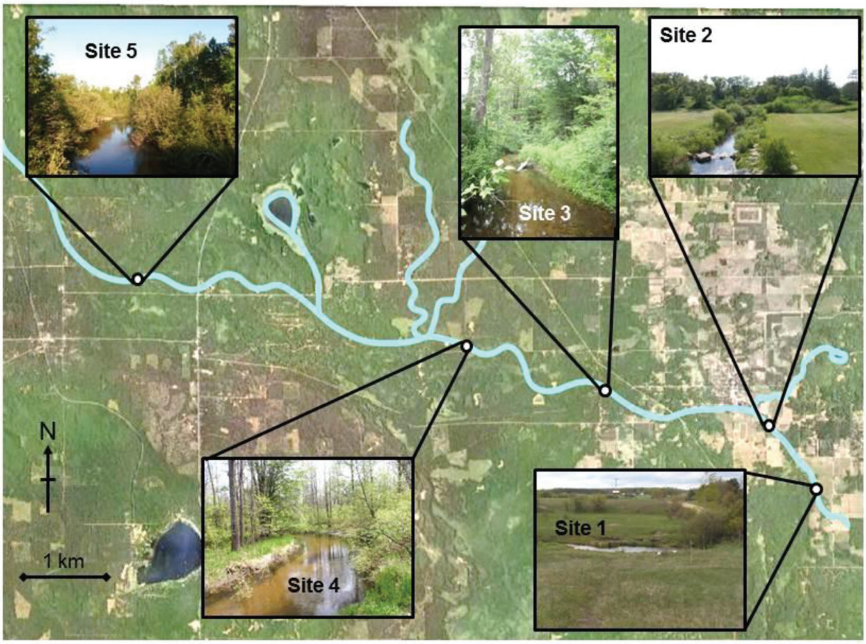

Figure. 1. Aerial photograph (Google Earth) of the study area showing the location of the Little Manistee River, its important tributaries, and the location and photographs of our five collecting sites. Green areas denote forest, whereas lighter brown areas denote agriculture, feral fields, or urban landuse.

within a stream reach of 10 km. All sites were upstream from major tributaries. Stream width ranged from 3 m (2nd order) in the upper sites to 10-12 m (4th order) at the lower sites. Determination of the extent of canopy cover was from aerial maps and visual inspection. Except for the occasional alder (*Alnus* sp.) along the banks, non-canopied areas of both streams were almost devoid of plants > 2 m in height within 100 m of either bank. Thus, the distinction between ‘canopied’ and ‘non-canopied’ sites was distinct enough that further quantification and precision were deemed unnecessary.

Physicochemical sampling. Physicochemical measurements were made twice during June and once monthly from July through September 2011. Six sets of measurements were made from each site on each date. Conductivity (ECTestr Low, Eutech Instruments), pH (AccuMet AP61, Fisher Scientific), dissolved oxygen (YSI-55, YSI Environmental), and temperature (YSI-55, YSI Environmental) measurements were all made on-site. All measurements were made within 2 h of each other to minimize diel fluctuations.

Benthic macroinvertebrate sampling. Benthic macroinvertebrates were sampled using Hess samplers with 0.3 m^2 areas (Barbour et al. 1999). Six Hess samples were taken from each site of each stream within a diversity of habitats. Sites 1, 2, and 4 were sampled during May 2010 and sites 3 and 5 were sampled in May 2011. All benthic specimens were identified to the lowest identifiable taxon, typically genus, after Hilsenhoff (1995).

Adult caddisfly sampling. Adult caddisflies were sampled using ultraviolet light traps, which consisted of an 8-watt ultraviolet light placed over a white pan filled with 70% ethanol. Each trap was placed within 2 m of a sampling site at dusk and retrieved approximately two hours later. By standardizing the time of collection, wattage of the light source, and size of collecting pan, the technique yielded quantitative samples of the nocturnally active caddisfly adults and allowed for comparisons between sites (Houghton 2004a). To standardize weather conditions, samples were collected only if the peak daytime temperature was > 22°C, dusk temperature was >13°C, and there was no noticeable wind or precipitation at dusk. Sampling occurred approximately bi-weekly during June and July 2011, the peak emergence period of caddisflies in northern Michigan (Houghton et al. 2011b), for a total of 5 samples from each site. All adult specimens were identified to species after Houghton (2012), except for females of Hydroptilidae, Hydropsychidae, and Polycentropodidae, which lack the characters necessary for doing so. Such specimens were not included in any analyses.

Data analyses. Specimens of both benthic invertebrates and adult caddisflies were placed into trophic functional groups following Merritt et al. (2008). Algal piercers were considered gathering collectors in analyses. Mean percentages of the functional groups informative of stream condition at each site: scrapers, shredders, and filtering collectors (e.g., Allan 1995, Houghton 2007), were compared to each other by a one-way Analysis of Variance. Percentages were transformed through an ArcSine function before analysis (Zar 2007). Mean water physicochemical values were compared using a 2-way Analysis of Variance to determine differences between both sampling site and sampling day.

Sampling sites were examined for patterns in their benthic macroinvertebrate and adult caddisfly assemblages with Detrended Correspondence Analysis (DCA) using the program PC-ORD for Windows® (McCune and Grace 2002). The DCA analysis was performed on a two-dimensional data matrix of sampling sites by taxa relative abundance values. Relative abundances were determined by counting the number of specimens collected at each site and then coding 0 specimens as ‘0’, 1–10 as ‘1’, 11–100 as ‘2’, 101–1000 as ‘3’, and 1001–10,000 as ‘4’. Since data coding accounted for variation in specimen abundance between sites, it was a more powerful measure than simple presence or absence data (Feminella 2000, Houghton 2004a). Coding on a $\log_{10}$ scale mitigated the effects

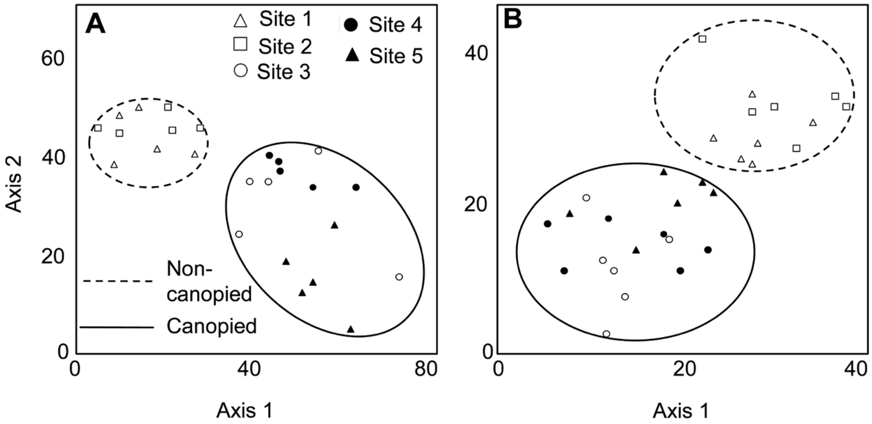

Figure 2. Detrended correspondence analysis ordination of (A) adult caddisflies, (B) benthic invertebrate samples from the Little Manistee River.

of outlier samples often associated with light-trapping data, as well as the influence of highly abundant species (Cao et al. 1997, Houghton 2004a, Houghton et al. 2011b). All taxa were weighted equally in each analysis.

Results

Assemblages of adult caddisflies and benthic invertebrates were different between sites with low riparian canopy and sites with higher canopy (Fig. 2); sites 1–2 appeared distinct from sites 3–5. Adult caddisfly filtering collector abundance was higher at sites 1–2 and lower at sites 3–5, although there were indistinct groups among the latter sites (Fig. 3). Shredder abundance was higher at sites 3–5, and lower at sites 1–2. Scraper abundance was unchanged between sites. The combined abundance of shredder, scraper, and filtering collectors was > 80% of total adult caddisfly specimens. Benthic invertebrates exhibited the same trends in shredder and filtering collector abundances: the former was more abundant at sites 3–5 and the latter was more abundant at sites 1–2 (Fig. 3). Scraper abundance was higher at sites 1–2 and lower at sites 3–5. All sites were dominated by gathering collectors (60–80%), and the combined abundance of shredder, scraper, and filtering collectors was ≤ 30% of total specimens at all sites (Fig. 3).

Individual filtering collector species were most abundant at sites 1–2, whereas shredder species were at their highest abundance at sites 3–5 (Table 1). The most abundant filtering collectors at the non-canopied sites were *Brachycentrus americanus* (Banks) (Brachycentridae), *Cheumatopsyche oxa* Ross, *Hydropsyche slossonae* Walker, and *H. sparna* Ross (Hydropsychidae). *Hydropsyche sparna* (Hydropsychidae), *B. americanus*, and *Lepidostoma togatum* Hagen were among the top 10 at all 5 sites.

Conductivity and pH exhibited no significant differences between sampling sites or between sampling dates (Fig. 4). Sites 1 and 2 had higher temperatures and lower dissolved oxygen than the other sites. Although there was significance between the temperature and dissolved oxygen values of different sampling dates in the overall model, there was also considerable overlap between these dates.

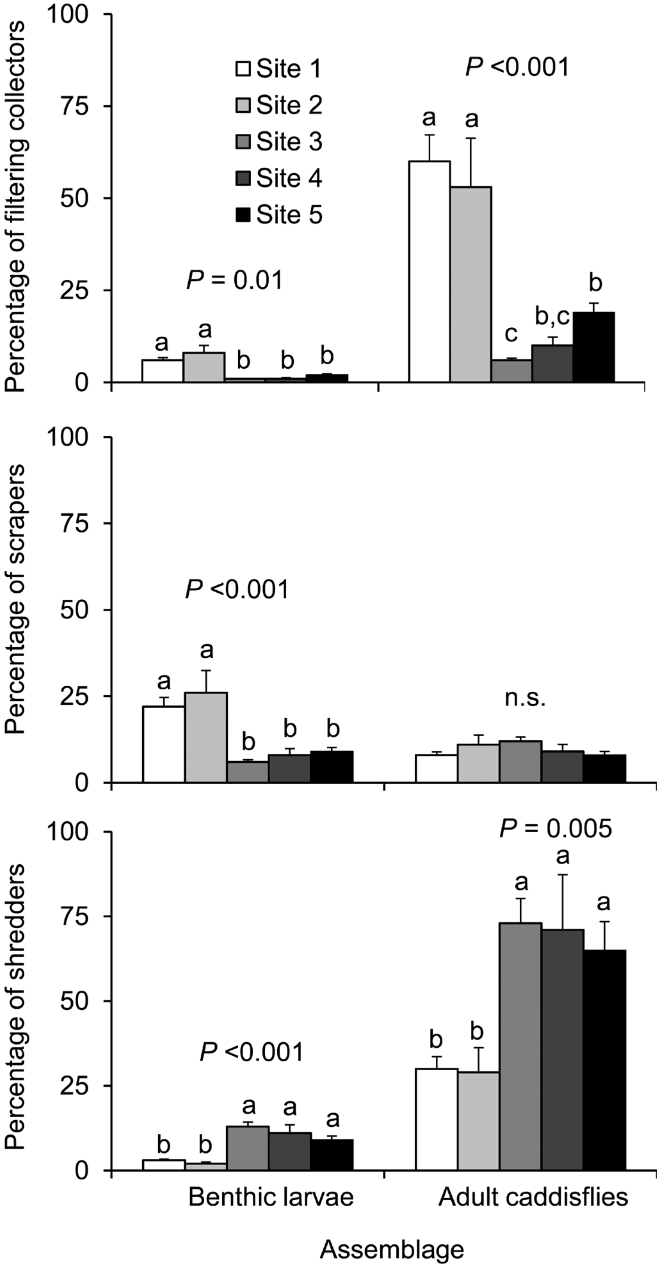

Figure 3. Mean (+SE) values of percentage of filtering collectors, scrapers, and shredders for benthic larvae and adult caddisflies of the Little Manistee River. Bars topped with the same lowercase letter were not statistically different (1-way Analysis of Variance with *post-hoc* Tukey test). n.s. = not significant.

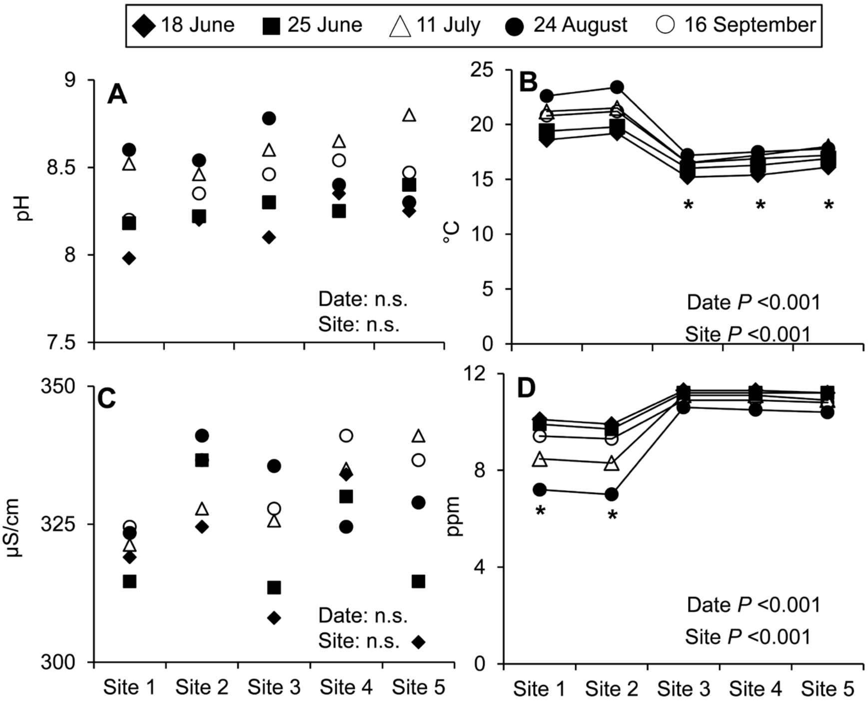

Figure 4. Mean physicochemical measurements determined on 5 different days from multiple sites of the Little Manistee River, with associated *P*-values (two-way Analysis of Variance). n.s. = not significant. Asterisks signify significantly different means between sites; one-way Analysis of Variance with (*post-hoc* Tukey test). (A) pH, (B) water temperature, (C) conductivity, (D) dissolved oxygen. Conductivity and pH displayed on expanded scale to show detail and with connecting lines omitted for clarity. Error bars omitted for clarity.

Discussion

The lack of riparian canopy at the upstream sites does not appear to have obvious effects on measured water physicochemistry. Conductivity and pH collectively have been found to explain nearly 80% of the watershed disturbance variation between sites of New Jersey watersheds, and were also associated with differences in organismal assemblages (Zampella and Laidig 1997, Dow and Zampella 2000). Conductivity, in particular, is often used as a preliminary indicator of nutrient, sediment, and organic matter concentrations. Such concentrations accumulate naturally in larger rivers, or anthropogenically in disturbed streams (Allan 2004). Michigan streams disturbed by agriculture have levels > 2× that of the Little Manistee (Castillo et al. 2000, Houghton et al. 2011a). Our low conductivity levels, as well as the lack of difference in both variables between study sites, suggested no important differences in natural or anthropogenic sediment input throughout the continuum.

It is difficult to judge the importance of temperature and dissolved oxygen differences between sites due to the differences in both variables between sampling dates. The temperature difference between sampling dates was similar (~5° C) to

Table 1. The 10 most abundant caddisfly species from 5 sites of the Little Manistee River.

		Species	**Functional group**	**Percentage of fauna**
Site 1	1	*Hydropsyche sparna* Ross	Filtering collector	31%
	2	*Hydropsyche slossonae* Banks	Filtering collector	20%
	3	*Cheumatopsyche oxa* Ross	Filtering collector	7%
	4	*Lepidostoma togatum* (Hagen)	Shredder	6%
	5	*Brachycentrus americanus* (Banks)	Filtering collector	4%
	6	*Neureclipsis crepuscularis* (Walker)	Filtering collector	3%
	7	*Lype diversa* (Banks)	Gathering collector	3%
	8	*Psychomyia flavida* Hagen	Gathering collector	2%
	9	*Glossosoma nigrior* Banks	Scraper	2%
	10	*Hydroptila consimilis* Morton	Gathering collector	2%
Site 2	1	*Hydropsyche sparna* (Ross)	Filtering collector	35%
	2	*Cheumatopsyche oxa* Ross	Filtering collector	18%
	3	*Cheumatopsyche gracilis* (Banks)	Filtering collector	8%
	4	*Hydropsyche slossonae* (Banks)	Filtering collector	6%
	5	*Neureclipsis crepuscularis* (Walker)	Filtering collector	5%
	6	*Psychomyia flavida* Hagen	Gathering collector	5%
	7	*Glossosoma nigrior* Banks	Scraper	4%
	8	*Hydroptila consimilis* Morton	Gathering collector	4%
	9	*Lepidostoma togatum* (Hagen)	Shredder	4%
	10	*Brachycentrus americanus* (Banks)	Filtering collector	3%
Site 3	1	*Lepidostoma togatum* (Hagen)	Shredder	30%
	2	*Lype diversa* (Banks)	Scraper	22%
	3	*Hydropsyche sparna* (Ross)	Filtering collector	10%
	4	*Brachycentrus americanus* (Banks)	Filtering collector	7%
	5	*Lepidostoma bryanti* (Banks)	Shredder	6%
	6	*Neureclipsis crepuscularis* (Walker)	Filtering collector	5%
	7	*Glossosoma nigrior* Banks	Scraper	4%
	8	*Nyctiophylax affinis* (Banks)	Predator	4%
	9	*Hydroptila consimilis* Morton	Gathering collector	3%
	10	*Hydroptila jackmanni* Blickle & Morse	Scraper	2%
Site 4	1	*Lepidostoma togatum (*Hagen)	Shredder	26%
	2	*Lepidostoma bryanti* (Banks)	Shredder	11%
	3	*Brachycentrus americanus* (Banks)	Filtering collector	9%
	4	*Lype diversa* (Banks)	Scraper	8%
	5	*Glossosoma nigrior* Banks	Scraper	6%
	6	*Neureclipsis crepuscularis* (Walker)	Filtering collector	5%
	7	*Nyctiophylax affinis* (Banks)	Predator	5%
	8	*Hydroptila jackmanni* Blickle & Morse	Scraper	3%
	9	*Cheumatopsyche gracilis* (Banks)	Filtering collector	3%
	10	*Hydropsyche sparna* (Ross)	Filtering collector	2%
Site 5	1	*Lepidostoma togatum* (Hagen)	Shredder	25%
	2	*Brachycentrus americanus* (Banks)	Filtering collector	16%
	3	*Lepidostoma bryanti* (Banks)	Shredder	14%
	4	*Psychomyia flavida* Hagen	Gathering collector	7%
	5	*Helicopsyche borealis* (Hagen)	Scraper	6%
	6	*Ceraclea transversa* (Hagen)	Gathering collector	5%
	7	*Hydropsyche sparna* (Ross)	Filtering collector	5%
	8	*Cheumatopsyche oxa* Ross	Filtering collector	4%
	9	*Lype diversa* (Banks)	Gathering collector	4%
	10	*Polycentropus pentus* Ross	Predator	4%

that between sampling sites. The observed differences between sites were likely due to the lack of canopy cover in the headwaters allowing additional sunlight to reach the stream surface and warm the water. Organisms at the canopied and non-canopied sites were probably exposed to slightly different temperature profiles. Dissolved oxygen typically exhibits a reciprocal relationship with temperature; thus, it was lower where temperature was higher in both streams (Allan 1995).

While the physicochemical differences between sites were unclear, our observed organismal assemblages suggested a reversal of predicted biological continuity. Continuity theory (Vannote et al. 1980) predicts high shredder abundance in low order (upstream) stream sites due to the high relative abundance of riparian canopy cover. Instead, Little Manistee shredders were more abundant at the higher order (downstream) sites. We suspect that this observation was due to canopy cover actually increasing in the downstream sites relative to the upstream sites, even though the Little Manistee obviously widens downstream (Fig. 1). Scrapers typically increase in abundance into the 4–5th order, and filtering collectors reach their highest abundances at the highest stream orders. In the Little Manistee, both functional groups instead decreased at the downstream sites.

While there have been many critiques and modifications of stream continuity theory (most recently Thorp et al. 2006), small woodland streams, such as the Little Manistee, do tend to follow the general predicted patterns if they are undisturbed (Allan 2004). Conversely, disturbed small woodland streams do not follow predicted patterns. Instead, they typically exhibit abundant filtering collectors and few shredders (Pringle et al. 1993; Delong and Brusven 1998; Houghton 2006, 2007). The abundance of filtering collectors alone accounted for nearly 70% of the watershed disturbance variation of small and medium streams in Minnesota (Houghton 2006). The overall assemblages of the upstream Little Manistee sites were those predicted from a medium-large river, despite a width of 3–4 m. More specifically, the relative abundances of adult caddisfly shredders and filtering collectors corresponded to those of 20–30 m wide Minnesota rivers (Houghton 2007). Once canopy cover returned downstream, however, continuity normalized and was maintained for the remainder of the studied stream length.

Even though filtering collectors dominated the non-canopied sites, these assemblages did not indicate ecosystems disturbed by excess sediment or nutrient input. Typically, a small stream with high levels of anthropogenic disturbance has an abundance of the specific filtering collector species that are normally found in large rivers. These species increase in disturbed small streams due to an abundance of fine particulate organic matter that they can utilize as a food source (Allan 1995, Barbour et al. 1999, Allan 2004, Houghton 2007). For example, the hydropsychid species *Cheumatopsyche campyla* Ross, *Hydropsyche simulans* Ross, and *Potamyia* flava Hagen are all typically found in large rivers of Minnesota, and only rarely in undisturbed small streams (Houghton 2012). In small agricultural streams, however, these same species were abundant and constituted significant indicators of disturbance statewide (Houghton 2004b). In the Little Manistee, all of the abundant filtering collectors (Table 1) were those naturally found in small woodland streams of the northcentral U.S. (Houghton et al. 2011b, Houghton 2012), albeit at lower relative abundances. Thus, instead of an increase in small-particle filtering collectors associated with large rivers and polluted small streams, our sites suggested a shift in the relative abundances of invertebrate assemblages already present. The normalization of continuity within ~3 km after canopy returned (between sites 2 and 3) also suggested the local effect of small-scale canopy loss, rather than systemic disturbance, such as sediment input or canopy removal on a large scale.

Our results also suggest relative strengths and weaknesses of using benthic macroinvertebrates and adult caddisflies to assess stream conditions. In the case of the former, nearly all of our sites were dominated by gathering collectors, which are common in nearly all habitat types and usually not informative of stream conditions (Vannote et al. 1980, Stagliano and Whiles 2002, Houghton 2007, Whiting et al. 2011). Thus, the high abundance of non-informative taxa relative to the informative scrapers, shredders, and filtering collectors may decrease the 'signal' relative to the 'noise' of a sample and render determination of stream conditions more difficult (e.g., Cao and Hawkins 2011). In the case of the latter, the lack of response from the scraper functional group has been noted in previous studies (Houghton 2006, 2007). While scraper taxonomic richness may be proportional within the Trichoptera (e.g., Wiggins 1996), scraper specimens are not generally abundant in blacklight samples relative to filtering collectors or shredders, or in benthic samples compared to taxa of other orders (Houghton 2012). Thus, the metric may not be abundant enough to be informative of stream conditions when using the Trichoptera exclusively.

Both of our assemblages reinforce the assertion that a loss of riparian habitat from ≥ 10 years ago can still impact stream biota (Harding et al. 1998). The potential mechanisms of this impact—such as decrease in allochthonous CPOM, increase in allochthonous FPOM, changes in substrate composition, increase in flooding, or other physiochemical factors—still need to be worked out. Year-round data logging would be beneficial to determine subtle difference in temperature between sites, as would more direct measurements of nutrients or suspended organic matter.

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