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The effects of landscape-level disturbance on the composition of Minnesota caddisfly (Insecta: Trichoptera) trophic functional groups: evidence for ecosystem homogenization

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Abstract Over 300,000 caddisfly specimens representing 249 species were collected from nearly 250 sites throughout Minnesota during 2000 and 2001 to determine the effects of human disturbance on the composition of caddisfly trophic functional groups at the landscape level. Canonical correspondence analysis determined that stream width was the most important variable influencing functional group composition in regions of the state with relatively low disturbance, and that differences in the caddisfly fauna between sizes of streams generally followed trends predicted by the river continuum concept. In regions of the state with moderate disturbance, both stream width and the percentage of disturbed habitat upstream of a site were important variables influencing functional group composition. In highly disturbed regions, no variables corresponded to changes in the composition of caddisfly functional groups. Instead, ecosystems were homogeneous: fine-particle filtering collectors dominated in all sizes of streams. The

observed aquatic ecosystem homogenization is attributed mostly to input of fine-particle organic and inorganic sediment from extensive agriculture.

Keywords Aquatic · Disturbance · Habitat · Feeding groups · Land use · Stream

Introduction

The caddisflies (Trichoptera) are valuable organisms for water quality biomonitoring due to their high species richness, ecological diversity, and abundance in virtually all types of aquatic habitats (Dohet 2002; Mackay and Wiggins 1979; Resh 1993; Rosenberg and Resh 1993; Wiggins 1996a, b). Many caddisfly species are classified as intolerant of habitat sedimentation and organic pollution (Barbour et al. 1999), thus a reduction in caddisfly species richness often occurs downstream of habitat disturbances (Berlin and Thiele 2002; Karr and Chu 1999; Kerans and Karr 1994). Some species, however, are tolerant of organic pollution and may increase in abundance downstream of a disturbance (Barbour et al. 1999). This phenomenon is pronounced in the filtering collector trophic functional group, as these organisms may utilize fine (<0.25 mm) organic particle input as a food resource (Barbour et al. 1999; Boiling et al. 1975; Cummins 1974; Wiggins 1996a, b). Logging, agriculture, and urbanization add organic material to aquatic ecosystems and may, therefore, promote an

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increase in the abundance of some filtering collector species while decreasing overall species richness (Allan 1995; Barbour et al. 1999; Gage et al. 2004; Kreatzweiser et al. 2005; Roth et al. 1996; Whiles et al. 2000).

In a previous paper (Houghton 2004a), I used detrended correspondence analysis and a flexible unweighted pair-group method using arithmetic averages algorithm to group 58 secondary watersheds in Minnesota into five regions of caddisfly biodiversity based on caddisfly relative abundance data (Fig. 1). Establishing these regions allowed the partitioning of the Minnesota caddisfly fauna into homogenous units with approximately double the classification strength of any *a priori* classification based on ecological data or primary catchment (Houghton 2003). Such regions, therefore, are likely the most appropriate units for sampling caddisflies within Minnesota (e.g., Hawkins et al. 2000a).

Further, I determined that the Northwestern and Southern caddisfly regions (Fig. 1) had significantly less species richness per sampling site than did the other regions due, in part, to the high level of human disturbance found in them (Houghton 2004a). A change in species richness frequently corresponds to changes in ecosystem functioning, specifically changes in the relative abundance of trophic functional groups such as shredders, scrapers, and filtering collectors (Cardinale and Palmer 2002; Cardinale et al. 2002; Cardinale et al. 2004; Huryn et al. 2002; Jonsson and Malmqvist 2003; Jonsson et al. 2001).

While many studies have documented impaired trophic functional group composition within a dis-

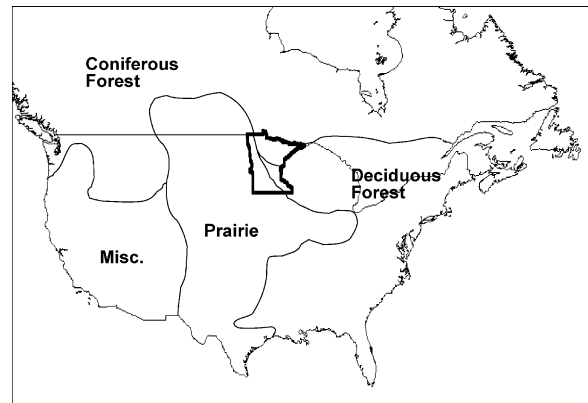


Fig. 2 The United States and southern Canada showing the convergence of the Coniferous Forest, Deciduous Forest, and Prairie biotic provinces within the state of Minnesota (Bailey 1980)

turbed stream reach (see Allan 1995; Karr and Chu 1999; or Covich et al. 2004), or within a single disturbed watershed (Allan et al. 1997; Allan 2004; Fausch et al. 2002; Townsend et al. 2003), none has examined such relationships on a large multi-watershed scale. If an entire landscape is modified into a large-scale land use such as agriculture – which is the case for much of the central US – then it is likely that the functioning of many large watersheds will be impaired. The objective of the present study was to detect potential changes in the composition of Minnesota caddisfly trophic functional groups with increases in the percentage of habitat disturbance on the landscape level. Due to the location of Minnesota at the intersection of the three largest biotic provinces of North America – Coniferous Forest, Deciduous Forest, and Prairie (Fig. 2) – and resulting habitat affinities with adjacent states and provinces, results should have a broad regional application.

Materials and methods

Sampling Aquatic habitats were divided into five stream classes based on stream width estimated from the sampling site (Table 1). Stream classes were constructed based on the approximate stream width divisions of the river continuum concept (RCC) (Vannote et al. 1980), thereby inferring ecological information about each site. At least four samples, representing one small stream (Class 1–2), one medium stream (3), and one large river (4–5) (Table 1)

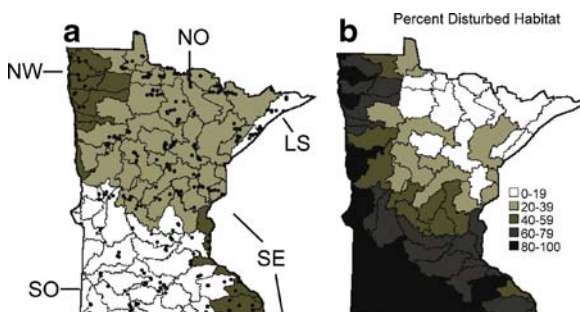


Fig. 1 **a** Watershed boundaries of the five caddisfly regions of Minnesota and the 248 sampling sites of this study. Overlap occurs between sample markers. *LS*: Lake Superior, *NO*: Northern, *NW*: Northwestern, *SE*: Southeastern, *SO*: Southern. **b** The relative level of disturbed habitat within the 58 major watersheds (USGS 1999)

Table 1 Five aquatic habitat classes and the total number of samples taken from each

| Class | Description | Width (m) | <i>n</i> |
|-------|---------------------|-----------|----------|
| 1 | Small stream | <2 | 24 |
| 2 | Small/medium stream | 2–4 | 37 |
| 3 | Medium river | 4–10 | 71 |
| 4 | Medium/large river | 10–30 | 54 |
| 5 | Large river | >30 | 20 |

Stream width was estimated at each sampling site.

were collected from most of the 58 major watersheds completely within Minnesota (Fig. 1). Watersheds lacking certain habitats, such as small streams or large rivers had sample sizes of three. Sampling sites were found using detailed sectional maps of Minnesota (DeLorme 1994), and were estimated to be the least disturbed of their respective watersheds based on observed upstream land use.

Caddisfly samples were collected during June and July, the peak period of adult emergence and flight activity in Minnesota (Houghton 2004a; Monson 1996). Adults were sampled at each site with an ultraviolet light trap, which consisted of an 8-watt portable ultraviolet light placed over a white pan filled with 70% EtOH. These traps were placed adjacent to aquatic habitats at dusk and retrieved approximately 2 h after dusk. While not an exhaustive technique since a few caddisfly species are day-flying or not attracted to lights, standardizing the time of collection, weather conditions, wattage of the light source, and size of collecting pan likely yielded a representative sample of the nocturnally active caddisfly adults and allowed for comparisons between sites (Houghton 2004a; Myers and Resh 1999; Nakano and Tanida 1999).

Several studies have suggested that most adult caddisflies disperse <100 m from the natal habitat (Petersen et al. 1999; Sode and Wiberg-Larson 1993; Sommerhäuser et al. 1999). Since virtually all of the sampling sites in this study were separated by >5,000 m, dispersal of adults between sites was assumed to be unimportant. To standardize weather conditions, samples were collected only on days with peak daytime temperature >22°C, dusk temperature >13°C, and no precipitation or noticeable wind at dusk (Anderson 1978; Anderson and Vondracek 1999; Houghton 2004a; Resh et al. 1975; Waringer 1989, 1991).

Caddisfly larvae were not collected during this study since larval collecting techniques are difficult to stan-

dardize, often fail to find rare species, and do not accurately represent all microhabitats (Barbour et al. 1999; Erman and Erman 1990; Merritt et al. 1996). Most larvae are not identifiable to the species level, resulting in a loss of information (Hawkins and Norris 2000; Hawkins and Vinson 2000; Hawkins et al. 2000a, b).

Data entry and calculations All specimens were identified to the species level except for females of some species of Hydropsychidae, Hydroptilidae, and Polycentropodidae, which lack characters necessary for species level identification. Such specimens were not included in any statistical analysis. All identified specimens were counted and entered into the relational database Biota (Colwell 2004). Locality and environmental data were exported from Biota to ArcView and Statistical Analysis System for Windows® software for further analyses (ESRI 1996; SAS Institute 1989). All specimens collected during this study were deposited in the University of Minnesota Insect Museum. Since samples were collected during two years, a Students *T*-test was performed on both mean species richness and mean specimen abundance among samples of each year to assess possible differences between years.

The relative abundance of five trophic functional groups: gathering collectors, filtering collectors, shredders, predators, and scrapers was compared between stream classes within each caddisfly region. Larval feeding preferences were determined at the genus level based on Wiggins (1996a, b). Algal piercers were considered to be gathering collectors (Cummins and Klug 1979; Wilzbach et al. 1988). The percentage of specimens within each group in a sample was determined for each individual sampling site, and means for a region were computed from these data. Four of the caddisfly regions were composed of a single biotic province (e.g., Coniferous Forest). The Southern region, conversely, was composed of both deciduous forest and prairie in approximately equal amounts (Figs. 1 and 2). Mean functional group abundance, therefore, was also determined for areas of deciduous forest and prairie within the Southern region separately.

Environmental analysis Continuous environmental variables potentially important to affecting trophic functional group composition were assessed with canonical correspondence analysis (CCA) (Ter Braak 1986, 1994), using PC-ORD for Windows® (McCune and Medford

1997). CCA is a direct multivariate gradient analysis which ordines a main data matrix (functional group composition data) based on a multiple regression on variables of a second matrix (environmental data), producing a plot of sampling sites in “trophic functional group space” (McCune and Medford 1997; Økland 1996; Rabeni and Doisy 2000). Because ordination of species data is constrained by the values of the environmental data, CCA excels at determining which variables are potentially important for predicting functional group composition, provided meaningful environmental data are measured (Økland 1996).

The main CCA data matrix consisted of the relative percentage of specimens within each of the five functional groups from each site. The second matrix was of sampling sites by the mean values of continuous environmental data for each site, which were selected *a priori* as potentially important in affecting caddisfly trophic functional group ecology. Latitude, longitude, and elevation were recorded with a hand held GPS unit or obtained from detailed topographical maps. Stream gradient was estimated visually at each site and placed into one of three classes – low, medium, high). Streams were divided into five classes as described earlier.

Human land uses such as agriculture, urbanization, mining, or intensive logging were determined from USGS (1999) data, and the amount occurring upstream of each sampling site was calculated using the “Tabulate Area” function of ArcView for Windows® software (ESRI 1996). The combined area of these land uses was expressed as the percentage of disturbed habitat. This measure has been shown to be an adequate descriptor of human effects, even without quantification of the severity of disturbance (Karr and Chu 1999). Furthermore, since the Twin Cities metropolitan area was excluded from the study, over 95% of the habitat disturbance was due to agriculture (USGS 1999), suggesting a similar severity of disturbance throughout sites.

Eigenvalues of the data axes determined by CCA were then correlated with functional group data and the determined *r*-values tested for significance using a Monte Carlo procedure in PC-ORD. Probability (*p*) values of the Monte Carlo test were estimated from the proportion of randomized runs with correlations between functional group data and environmental values greater than or equal to the observed correlation of the data set (McCune and Medford 1997). CCA also reported *r*-values between axis scores and values of

specific environmental variables. The significance of a particular environmental variable was assessed by its association with data axes (Houghton 2004a; Kremen 1992; Ter Braak and Prentice 1988). CCA analyses were conducted for sites within each of the five Minnesota caddisfly regions.

Results

A total of 306,541 caddisfly specimens were collected from 248 aquatic habitats within 58 Minnesota watersheds (Fig. 1); 134 samples were collected in 2000 and 114 in 2001. There was no significant difference in either mean species richness ($p=0.40$) or mean specimen abundance ($p=0.10$) among samples over the two years of this study (Students *T*-test), suggesting that potential differences across years were unimportant.

In the Lake Superior region, CCA detected two axes with significant correlations between functional group composition and environmental data (Table 2). A third determined axis was not significant. Because these axes explained over half of the variance in the species matrix, it is unlikely that additional axes would have been highly informative (McCune and Medford 1997). Axis 1 correlated most strongly with stream class. No specific variable correlated with axis 2. The analysis also suggested four clusters of sites corresponding to stream class – no large rivers were found in this region (Fig. 3).

In the Southeastern regions, CCA detected two significant axes. Both stream class and percentage of disturbed habitat correlated with axis 1 (Table 2). No specific variable correlated with axis 2. The analysis also suggested four clusters of sites corresponding to stream class – no natural lakes were found in this region (Fig. 3).

In the Northern region, CCA detected two significant axes. Stream class correlated with axis 1, and percentage of disturbed habitat correlated with axis 2 (Table 2). The analysis suggested five clusters of sites corresponding to stream class, although medium and small-medium streams clustered together, and there were five outlier small-medium to medium-large streams that clustered with large rivers (Fig. 3).

In the Lake Superior, Northern, and Southeastern regions, changes in the relative abundance of trophic functional groups exhibited trends predicted by the RCC (Fig. 4). Shredders had the highest relative

Table 2 Correlation coefficients between six environmental variables and two significant axes of ecological interest based on canonical correspondence analysis of environmental data and caddisfly trophic functional group relative abundance in five Minnesota caddisflies regions

| Variable | Lake Superior | | Northern | | Southeastern | | Southern | | Northwestern | |
|--------------|---------------|--------|--------------|--------|--------------|--------|----------|--------|--------------|--------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Latitude | 0.22 | −0.19 | −0.13 | −0.10 | 0.32 | −0.35 | 0.12 | 0.11 | −0.28 | 0.14 |
| Longitude | 0.14 | 0.11 | −0.20 | 0.09 | 0.25 | −0.12 | −0.25 | 0.14 | −0.26 | −0.19 |
| Elevation | −0.23 | 0.17 | 0.12 | 0.14 | 0.13 | 0.08 | 0.32 | 0.18 | −0.08 | −0.31 |
| Gradient | −0.31 | 0.20 | −0.25 | 0.32 | 0.29 | −0.34 | −0.18 | 0.19 | 0.16 | 0.23 |
| Stream class | <i>0.87</i> | −0.41 | <i>−0.86</i> | 0.38 | <i>−0.84</i> | 0.22 | 0.21 | −0.20 | −0.33 | 0.25 |
| % disturbed | 0.21 | 0.30 | 0.19 | −0.78 | −0.82 | 0.16 | 0.39 | −0.17 | −0.42 | 0.20 |
| S^2 | 0.74 | 0.17 | 0.52 | 0.31 | 0.63 | 0.22 | 0.44 | 0.32 | 0.48 | 0.28 |

Italicized coefficients (>0.500) were deemed important. The “variable” S^2 refers to the amount of variance explained by each axis and is not an actual environmental variable.

abundance in small-medium streams (Classes 1–3). Shredders decreased in abundance relative to the other feeding groups as stream width increased. Filtering collectors increased in relative abundance as stream width increased and had the highest mean abundance

in medium and large rivers (Class 4–5). Predators and scrapers exhibited low-moderate relative abundance in all site classes and did not show a clear trend. Gathering collectors had moderate to high relative abundance in all sizes of streams.

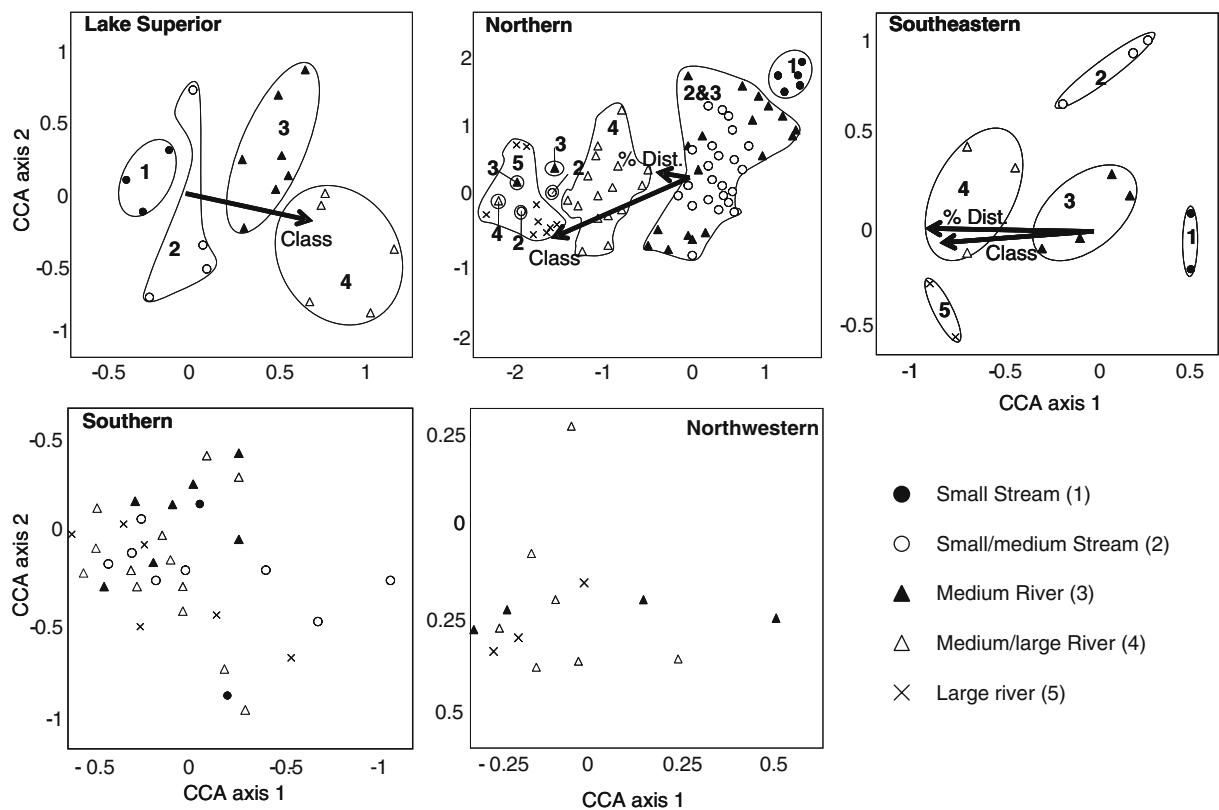


Fig. 3 Canonical correspondence analysis biplot ordination of sampling sites within five caddisfly regions of Minnesota. Arrow(s) indicate strength and direction of gradient

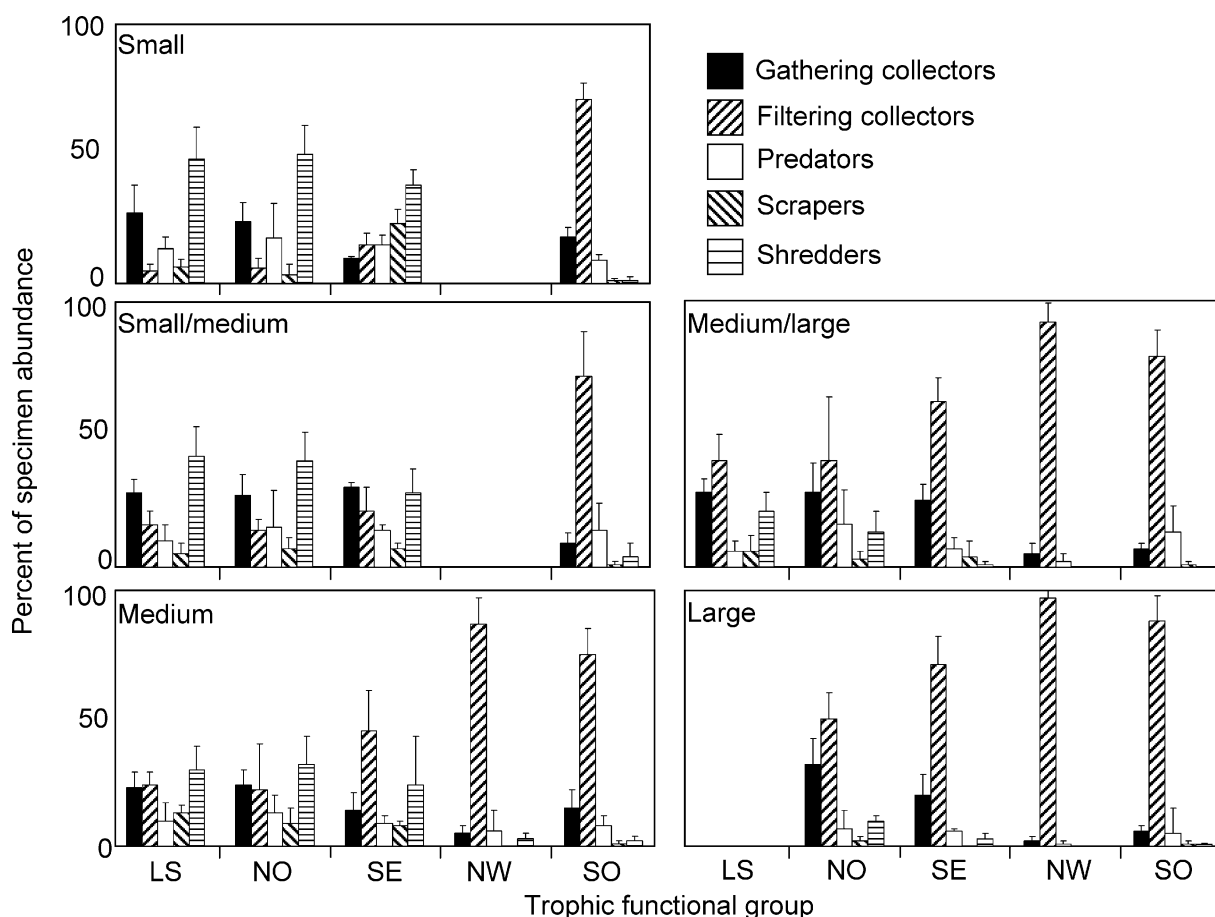


Fig. 4 Percentage of mean (\pm SE) specimen abundance for five trophic functional groups (Wiggins 1996a, b) within five different stream classes (Table 1) of the Lake Superior (LS),

Northern (NO), Southeastern (SE), Northwestern (NW), and Southern (SO) caddisfly regions (Fig. 1)

In the Northwestern and Southern regions, CCA detected two significant axes for each; however, no specific variables correlated with any axis. Likewise, there did not appear to be any distinct pattern of site clustering. Filtering collectors had the highest mean abundance in all site classes within both regions (Fig. 4), and in both Prairie and Deciduous Forest areas of the Southern region (Fig. 5). The other functional groups all exhibited a low to moderate relative abundance in all site classes.

Discussion

The river continuum concept (RCC) describes a predictable pattern of changes in the composition of aquatic insect trophic functional groups as stream width increases (Merritt et al. 1984; Vannote et al.

1980). Thus, if the aquatic ecosystems in this study were functioning as predicted, then patterns in functional group composition should be obvious between streams of different width within each homogenous caddisfly region, and other variables should be of minimal importance.

Such a pattern existed within the Lake Superior, Northern, and Southeastern regions (Fig. 3). In the Lake Superior region – the least disturbed of all regions (Fig. 1) – all four stream classes clearly separated into clusters and only one variable-stream class – correlated with the observed caddisfly functional group composition. Similar patterns were exhibited in the Northern and Southeastern regions, albeit not as clearly. Sampling sites still grouped into clusters correlating with stream classes; however, clusters also correlated with percent habitat disturbance. Over 50% of the Southeastern region is disturbed; however, many of the

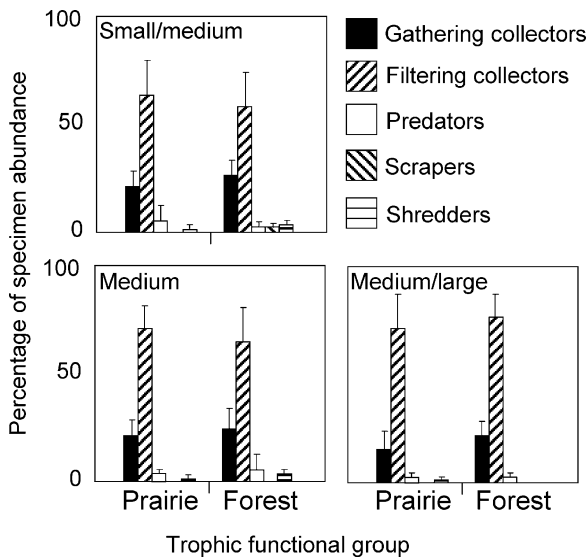


Fig. 5 Percentage of mean (\pm SE) specimen abundance for five trophic functional groups (Wiggins 1996a, b) within three different stream sizes (Table 1) of areas of prairie and deciduous forest within the Southern caddisfly region (Fig. 1). Classes with sample sizes <2 were omitted

forested watersheds of the small to medium-sized streams are protected by the state park system while the habitats of larger rivers are not. Thus, larger streams tend to be more disturbed, leading to the correlation between site class and habitat disturbance on the same axis (Table 2). In the Northern region, stream class and percent disturbed habitat both correlated with functional group composition, but on different axes. Most watersheds of the northern region are $<10\%$ disturbed; however some are $>20\%$ disturbed (Fig. 1). The correlation of the percent disturbed habitat with functional group composition is due primarily to five “outlier” sampling sites: small-medium streams of high disturbance that clustered with large rivers. The functional group composition of the Southern and Northwestern regions did not appear to exhibit any type of clustering pattern, nor did any variable correlate with functional group composition (Fig. 3).

In the Lake Superior, Northern, and Southeastern regions, relative abundance of trophic functional groups – particularly the changes in relative abundance of shredders and filtering collectors – followed a general pattern predicted by the RCC (Fig. 4). According to the RCC, shredders are most abundant in small streams (Class 1–2), because the canopy of riparian vegetation over the narrow stream channel promotes high levels of coarse allochthonous input.

Scrapers typically exhibit their highest abundance in medium-sized streams (Class 2–3) because the widening stream allows more solar radiation to stimulate growth of periphyton. In large rivers (Class 4–5), filtering collectors typically exhibit high abundance as the breakdown of detritus from upstream areas promotes high levels of their fine particle food source. Predators typically show little change in abundance in different ecosystems as their primary food source is common in all types of lotic and lentic systems. The preferred food type of gathering collectors – substrate-deposited organic material – is also common in all types of aquatic ecosystems, hence gathering collectors usually exhibit high abundance in all ecosystem types.

It is unlikely that the functional group composition in the Lake Superior, Northern, and Southeastern regions is completely “natural.” Many of the watersheds throughout the U.S. that are now forested have been previously logged or cultivated, with resulting loss of woody debris and sediment, and floodplain and channel modification, effects that may last for 10s or 100s of years (Allan 2004; Bierley et al. 1999; Johnson et al. 2003; Naiman et al. 1998; Perkins 1994). Likewise, much of Minnesota has been previously disturbed, and these previous disturbances were not taken into account in the USGS (1999) database. How much effect historical disturbance has on contemporary functional group composition is not clear. In a study of Appalachian forests, Harding et al. (1998) found that the biological diversity of former agricultural landscapes was more similar to that of current agricultural landscapes than it was to that of primary forest. Wang et al. (2001) attributed differences in fish diversity along an urbanization gradient to the effects of prior agriculture along the stream. Conversely, Wang et al. (2003) found that anthropogenic disturbance was less important than natural features in predicting fish assemblages within the relatively undisturbed ecosystems of northern Michigan and Wisconsin, a landscape similar to that of northern Minnesota. Allan (2004) suggests that when human disturbance is “minor,” functional group composition is more affected by natural factors – such as stream width – than by land use. This situation probably occurs in the Lake Superior, Northern, and portions of the Southeastern regions of Minnesota.

In obvious contrast, the trends in functional group composition between sites of the Northwestern and Southern regions strongly suggest ecosystem homog-

enization on a landscape level. Filtering collectors dominated in all site classes including small streams (Fig. 4), which suggests that fine organic particles are present at a higher abundance in such ecosystems than would be expected based on habitat type. A similar phenomenon likely occurs in the five “outlier” streams with higher disturbance of the Northern region that clustered with large rivers (Fig. 3).

The observed homogenization in the Northwestern and Southern regions is likely due to human disturbance, specifically the effect of agriculture. Intensive agriculture probably has the most extensive impact of any human land use on aquatic ecosystems (Allan 1995, 2004; Karr and Schlosser 1978; Karr et al. 1985; Omernik 1977; Sponseller et al. 2001; Wang et al. 1997; Williams et al. 2003; Zimmerman et al. 2003). Agriculture often leads to stream channelization, draining of wetlands, modification or loss of the surrounding floodplain, and removal of riparian canopy cover with subsequent loss of coarse allochthonous input (Allan 1995; Delong and Brusven 1998; Gregory et al. 1991; Lowe-McConnell 1987; Quinn 2000). Agricultural runoff into aquatic habitats often contains large amounts of sediment and fine organic matter (Gianessi et al. 1986; Turner and Rabalais 1991; Zweig and Rabeni 2001). Collectively, these impacts promote homogenization of stream microhabitats and an increase in autotrophic production, especially in small to medium streams. Essentially, small streams develop the characteristics of large rivers (Berkman and Rabeni 1987; Delong and Brusven 1992, 1993; Feminella et al. 1989; Houghton 2004b; Pringle et al. 1993). The Northwestern and Southern regions are dominated by agricultural land use, whereas much of the Northern, Lake Superior, and portions of the Southeastern region are composed of forest (USGS 2002).

It is possible that the atypical trophic functional group composition could have been caused by the predominance of prairie ecosystems in the Northwestern and Southern regions. Several authors (Dodds et al. 1996; Gray 1997; Statzner and Higler 1985; Wiley et al. 1990) have suggested that streams within natural prairie ecosystems do not fit into the RCC model; instead exhibiting increasing canopy cover into the middle stream reaches (Class 3). Erosion of nutrient-rich prairie soil may lead to naturally high levels of dissolved nitrogen and phosphorous in prairie streams (Anderson and Grigal 1984; Buol et al. 1989). The combination of limited canopy cover and high

nutrient availability may promote ecosystem autotrophy, a lower than expected abundance of shredders, and a higher than expected abundance of filtering collectors in small and medium streams (Class 1–3) of the Northwestern and Southern regions.

Covariance between natural and anthropogenic variables is frequently a problem in ecological studies (Allan 2004), and separating the two influences on modern Minnesota prairie aquatic ecosystems is difficult. Almost all of the prairie vegetation has been removed and replaced by agricultural environments and only small prairie remnants remain, precluding a watershed-level analysis (Tester 1995). Filtering collectors, however, had a high relative abundance in all streams in both prairie and deciduous forest areas of the Southern caddisfly region, which suggests that natural differences between these areas are less important than contemporary land use factors in affecting trophic functional group composition (Fig. 5).

Similar results – specifically, widespread disturbance overwhelming natural variation – have been found in other agriculturally-impacted streams (Allan 2004; Delong and Brusven 1998; Johnson et al. 1997). In Kansas, an undisturbed headwater (Class 1) prairie stream was dominated by gathering collectors, whereas filtering collectors composed <10% of organismal abundance (Stagliano and Whiles 2002). Wiley et al. (1990) found that agricultural and urban land use contributed more nutrient input into prairie streams in Illinois than did natural processes. Several studies of the Red River of the North basin – a mainly prairie ecosystem approximating the boundaries of the Northwestern caddisfly region – have determined that insect and fish populations are affected by nutrients and fine sediment related to agricultural cultivation (Goldstein 1995; Goldstein et al. 1996; Stoner et al. 1993, 1998).

It is likely, therefore, that agricultural environments – and their corresponding physical and chemical changes to the watershed – are important influences on caddisfly functional group composition of small-medium streams within Minnesota. It is difficult to hypothesize if large rivers are also affected, since abundance of filtering collectors is predicted by the RCC in such habitats. The inclusion of other aquatic insect taxa or a calculation of the relative biomass of trophic functional groups would undoubtedly add value to these findings. The numerical differences of caddisfly trophic functional groups alone, however, were remarkable considering the diversity and abundance of the order.

Potential implications This study suggests that an increase in sediment and organic matter input from large-scale agriculture is changing the community structure of caddisflies within entire regions of Minnesota. While such a suggestion is probably not surprising, if it holds true, the implications are potentially far-reaching. Large-scale agriculture occurs over much the central United States, including more than 90% of the Prairie biotic province, 95% of the Minnesota River basin, and nearly 70% of the upper Mississippi River basin (Allan 2004; Benke and Cushing 2004; Tester 1995). Assuming the primary mechanism of ecosystem disruption – increased sediment and organic matter input – is similar throughout disturbed regions, aquatic ecosystems in large portions of the United States have probably lost their natural ecological functioning. Ecological implications of such changes likely include loss of many of the services provided by a properly functioning aquatic ecosystem (e.g., Meyer 1997), as well as a large repository of genetic diversity.

In some regions of Minnesota, the degree to which ecological function was affected on a landscape level appeared to be influenced by the occurrence of “refuge” habitats: relatively undisturbed ecosystems within a large disturbed area. The land area of the Southeastern region, for example, is over 50% disturbed (Fig. 2). The state park system, however, protects the forested headwaters of several small and medium streams within the larger disturbed watersheds. Such refuge habitats were sampled in this study and trophic function of this region, therefore, was as expected (Fig. 4). In contrast, it was difficult to locate refuge habitats within the Southern region, and impossible to locate them in the Northwestern region. Agricultural and small urban habitats dominated the entire landscape in these areas. Not only did trophic function appear impaired, but species richness per watershed was significantly less than that of the Lake Superior, Northern, or Southeastern regions (Houghton 2004a).

Expanding this research to states and provinces with large-scale agricultural disturbance, especially within the Prairie biotic province, is an important future endeavor, as is the search for refuge habitats within these areas. Expanding to other aquatic taxa is likewise important; the consistently low abundance of predators and scrapers in this study, for example, suggests that some ecological diversity was missed by using only the Trichoptera. Within Minnesota, research addressing the biological fate and quantifiable

effects of sediment and organic matter on aquatic organisms would confirm the findings of this study, and would help clarify effects of human land use on aquatic ecosystems.

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