

Functional redundancy of stream macroconsumers despite differences in catchment land use

K. A. SCHOFIELD, C. M. PRINGLE, J. L. MEYER AND E. J. ROSI-MARSHALL

Institute of Ecology, University of Georgia, Athens, GA, U.S.A.

SUMMARY

1. The conversion of forested landscapes to agriculture and, increasingly, to suburban and urban development significantly affects the structure and function of both terrestrial and aquatic ecosystems. While a growing body of research is examining how biotic communities change in response to human alteration of landscapes, less is known about how these changes in community structure affect biotic interactions.
2. The objective of this study was to examine top-down control by macroconsumers (fish and crayfish) across a human-impacted landscape. We predicted that changes in stream macroconsumers and physicochemical characteristics associated with increased catchment development (e.g. decreased abundance of fish that are obligate benthic invertivores, increased sedimentation) would diminish top-down control of benthic insects. We expected that effects on algal assemblages would be more variable, with increased top-down control at sites dominated by algivorous fish and diminished control elsewhere. To test these predictions, we experimentally excluded fish and crayfish from areas of the bed of five streams whose catchments ranged from 100% to <50% forested, and examined the effects of exclusion on benthic insects and algae.
3. Despite cross-site differences in physical, chemical and biological characteristics, the outcome of our experiments was consistent across five sites representing a range of catchment development. Across all sites, macroconsumers reduced total insect biomass, largely due to decreases in Chironomidae and Hydropsychidae larvae. Macroconsumers also affected algal assemblages, reducing chlorophyll-*a* and the proportion of upright and filamentous diatoms (e.g. *Melosira*, *Cymbella*) but increasing the proportion of adnate diatoms (e.g. *Achnanthes*) across all sites.
4. We expected that differences in factors such as macroconsumer assemblage composition, nutrient and light availability and sedimentation would result in variable responses to macroconsumer exclusion in the five streams. Contrary to these expectations, only one response variable (ash-free dry mass) showed a statistically significant interaction (i.e. site \times exclusion) effect. Most responses to exclusion were relatively consistent, suggesting functional redundancy in assemblages of macroconsumers among the sites despite differences in catchment land use.

Keywords: electric exclusion, land use, redundancy, streams, top-down

Correspondence: K. A. Schofield, National Center for Environmental Assessment, U.S. Environmental Protection Agency, Washington, DC 20460, U.S.A. E-mail: schofield.kate@epa.gov

Present address: E. J. Rosi-Marshall, Department of Biology, Loyola University, Chicago, IL 60626, U.S.A.

Introduction

The conversion of natural landscapes to agricultural use and, increasingly, to suburban and urban development alters the physical, chemical and biological characteristics of ecosystems (McDonnell & Pickett, 1990; Paul & Meyer, 2001; Allan, 2004). One common effect of development is the alteration of assemblage structure, measured as the abundance, diversity and composition of species found within a system. A growing body of research in both terrestrial and aquatic environments is examining how biotic communities change in response to land use (McKinney, 2002; Walsh *et al.*, 2005), but few studies have examined how such development affects biotic interactions (McDonnell & Pickett, 1990). Although many ecological studies have demonstrated the importance of top-down processes in structuring biotic communities, and that the outcome of these interactions depends on the abiotic and biotic environment (e.g. Dunson & Travis, 1991; Hunter & Price, 1992), little research has experimentally addressed how the many effects of land use change cumulatively affect consumer control in streams (Paul & Meyer, 2001).

Such land use changes offer opportunities to examine the factors influencing top-down effects. In streams, for example, certain fishes tend to decrease in disturbed catchments: taxa which feed on benthic invertebrates and require clean substrata for spawning (e.g. sculpins, darters) often are replaced by algivores and by omnivores that can feed both from the benthos and the water column, and by taxa which can spawn in fine sediments (e.g. minnows and sunfishes) (Schlosser, 1982; Harding *et al.*, 1998; Sutherland, Meyer & Gardner, 2002). This replacement of specialist predatory fish (i.e. obligate benthic invertivores) by more generalist species suggests differences will exist in top-down control of benthic invertebrates and algae across a gradient of catchment disturbance. If fish with different feeding habits are not ecologically equivalent in terms of their top-down effects, we would expect low functional redundancy of fish consumers across streams varying in surrounding land use (Walker, 1992; Rosenfeld, 2002).

However, fish are not the only component of ecosystems altered by land use change. Many changes in the physical, chemical and biological environment accompany agricultural, suburban and urban development, and these changes can simultaneously

influence consumer impacts, often in contradictory ways. In streams, for example, sedimentation frequently increases with catchment development and can weaken consumer effects (Peckarsky, 1985; Schofield, Pringle & Meyer, 2004). In contrast, riparian canopy cover is often reduced by human activity, increasing irradiation, algal production and consumer effects (Wellnitz & Ward, 1998). By studying top-down interactions in human-modified systems *in situ*, it is possible to examine how the numerous abiotic and biotic shifts associated with development *cumulatively* influence the strength and outcome of consumer effects.

The objective of this study was to examine top-down control by macroconsumers (fish and crayfish) across a human-impacted landscape. We predicted that changes in macroconsumer assemblages, and in the physicochemical characteristics associated with catchment development, would diminish top-down control of benthic insects. We expected that effects on algal assemblages would be more variable, with increased top-down control at sites dominated by algivorous fish and reduced control at sites dominated by non-algivorous taxa. To test these predictions, we experimentally excluded fishes and crayfishes from areas of the bed of five streams whose catchments ranged from 100% to <50% forested, and examined the effects of the exclusion on benthic insects and algae.

Methods

Study sites

Experiments were carried out in the southern Appalachian Mountains of western North Carolina, a region supporting diverse stream communities, including many endemic and endangered species (e.g. Cooper & Braswell, 1995; Scott & Helfman, 2001). Diversity in this region is threatened by human population growth and development: the human population has increased by more than 30% over the last three decades, with a decline in agricultural land use and an increase in residential and commercial development (SAMAB, 1996). Much of this development has occurred on land adjacent to streams (Bolstad & Swank, 1997), providing an ideal opportunity to examine how land use change influences the outcome of species interactions in lotic systems.

Over the past decade, researchers at the Coweeta Long Term Ecological Research (LTER) site have collected physical, chemical and biological data in 36 southern Appalachian streams differing in catchment land use (e.g. Harding *et al.*, 1998; Jones *et al.*, 1999; Scott & Helfman, 2001; Scott, 2006). In this paper, we focus on five of these streams (Fig. 1), located in the Little Tennessee River basin (Lower Ball Creek and Jones Creek; hereafter 'Forest 1' and 'Agriculture', respectively) and the French Broad River basin (Upper Davidson River, Beaverdam Creek and Sweeten Creek; hereafter 'Forest 2', 'Suburban' and 'Urban', respectively).

Sites were selected in areas that varied in extent and type of catchment development, resulting in significant among-site differences in both physical and chemical characteristics (Table 1) and biotic assemblages, particularly in terms of macroconsumers (Table 2). In general, physicochemical measures (e.g. nutrient concentrations, water temperature, water conductivity) increased from relatively unaltered sites (Forest 1 and Forest 2) to those more affected anthropogenically (Suburban and Urban); canopy cover showed the opposite trend, decreasing in more developed catchments (Table 1). Water velocity, water depth and shear stress differed across sites but did not show consistent patterns with development (Table 1).

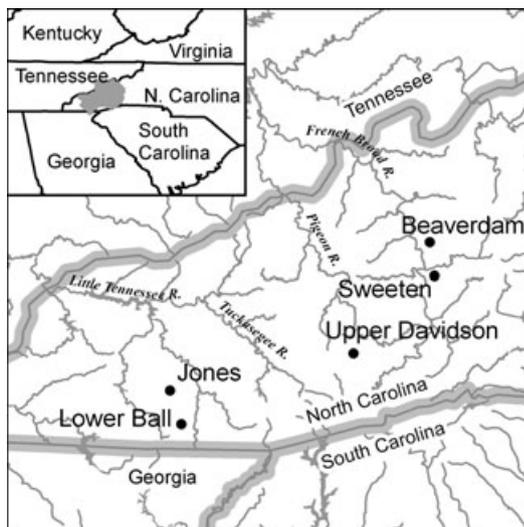


Fig. 1 Location of five study sites in western North Carolina, U.S.A. Lower Ball Creek (Forest 1) and Jones Creek (Agriculture) are part of the Little Tennessee River drainage; the Upper Davidson River (Forest 2), Beaverdam Creek (Suburban) and Sweeten Creek (Urban) are part of the French Broad River drainage.

Amounts of sediment were significantly different across sites, both in terms of total suspended solids (TSS) and deposited sediment. Concentrations of TSS were at least twice as high at Urban than at the other four sites, and deposited sediments showed even greater cross-site differences (Table 1). Sediment was relatively sparse at Forest 1, Forest 2 and Agriculture, but was significantly greater at both Suburban and Urban; for example, the amount of deposited sediment at Urban was more than 300-times higher than at Forest 2.

Macroconsumer assemblages were dominated by mottled sculpin (*Cottus bairdii* Girard), an obligate benthic invertivore, and omnivorous crayfish (*Cambarus bartonii* Fabricius, *C. robustus* Girard and *C. georgiae* Hobbs) at Forest 1, Forest 2 and Agriculture (Table 2). Omnivorous crayfish (*C. bartonii* and *C. robustus*) also were collected at Suburban and Urban, but fish assemblages were dominated by the algivorous central stoneroller (*Camptostoma anomalum* Rafinesque) at Suburban and a mix of generalized invertivores [e.g. Tennessee shiner (*Notropis leuciodus* Cope), warpaint shiner (*Luxilus coccogenis* Cope), creek chub (*Semotilus atromaculatus* Mitchell)] at Urban (Table 2).

Experimental design

During the summers of 1997 and 1998, 40-day electric exclusion experiments were performed at the five study sites (two sites in 1997, three sites in 1998). All experiments were carried out at baseflow conditions and, other than brief, infrequent periods of rainfall, significant storms did not occur during the experiments in either year. There was some variability in rainfall across the five sites, but inter-annual variability was no greater than intra-annual variability (Table 1).

Unglazed brown ceramic tiles (7.5 × 15 cm) were attached with cable ties and binder clips to polyvinylchloride (PVC) frames (0.25 m²) lined with copper wire; each frame contained six or eight tiles. Ten PVC frames (five pairs) were anchored to the stream bottom in run habitats at each site. Placement of pairs was determined by preliminary shear stress measurements taken with calibrated hemispheres (Statzner & Müller, 1989). Water velocity and depth were measured with a Marsh McBirney® current meter (Marsh McBirney, Inc., Frederick, MD, U.S.A.) and a metre stick at the four corners of each frame. Canopy cover

Table 1 Site characteristics at the five study sites

Parameter	Forest 1	Forest 2	Agriculture	Suburban	Urban
Duration of experiment	7/29–9/8/1997	6/29–8/8/1998	7/31–9/9/1997	7/1–8/10/1998	6/30–8/9/1998
Precipitation (in)*	2.70	2.31	2.24	1.48	1.73
Catchment characteristics					
Area (ha)	711	1830	4317	1927	1401
Altitude (m)	689	791	665	644	604
Distance to head waters (km)	3.96	5.74	10.06	6.39	6.88
% Forested – total	100	100	95	88	41
% Non-forested – 30 m buffer [†]	0	0	14	21	60
Physical parameters					
Canopy cover (%)	85.9 (1.0) ^a	77.1 (4.9) ^{ab}	59.1 (3.2) ^c	67.8 (5.7) ^{bc}	16.1 (2.5) ^d
Water depth (m)	0.17 (0.01) ^{ab}	0.20 (0.02) ^b	0.20 (0.01) ^b	0.12 (0.01) ^c	0.14 (0.01) ^{ac}
Water velocity (m s ⁻¹)	0.23 (0.01) ^a	0.12 (0.02) ^b	0.33 (0.02) ^c	0.20 (0.01) ^a	0.16 (0.02) ^{ab}
Shear stress (dyn cm ⁻²)	86.4 (2.8) ^a	80.3 (7.8) ^a	149.9 (7.2) ^b	54.7 (0) ^a	77.4 (8.2) ^a
Physicochemical parameters					
Water temp (°C) [‡]	17.5 (0.2) [41] ^a	18.1 (0.1) [38] ^b	n.a.	22.8 (0.1) [40] ^c	23.3 (0.2) [40] ^c
Temp range (°C) [§]	1.2 (0.1) [41] ^a	1.7 (0.1) [38] ^b	n.a.	4.1 (0.2) [40] ^c	3.5 (0.1) [40] ^d
Deposited sediment (g m ⁻²) [¶]	141 (28.1) [5] ^a	56.2 (9.40) [5] ^a	274 (143) [5] ^a	2090 (888) [4] ^b	17200 (6620) [5] ^c
TSS (mg L ⁻¹)	7.5 (0.4) [40] ^a	4.5 (0.3) [7] ^a	8.0 (0.5) [40] ^a	10.1 (1.7) [8] ^a	20.8 (4.3) [8] ^b
Conductivity (µS cm ⁻¹)	13.5 (0.0) [3] ^a	14.5 (0.1) [7] ^a	33.6 (0.3) [3] ^b	71.7 (0.9) [6] ^c	109 (1.8) [7] ^d
NO ₃ -N (mg L ⁻¹)	0.04 (0.00) [9] ^a	0.13 (0.00) [7] ^b	0.10 (0.01) [9] ^c	0.33 (0.01) [6] ^d	0.86 (0.04) [7] ^e
NH ₄ -N (mg L ⁻¹)	0.003 (0.001) [9] ^a	0.003 (0.000) [7] ^a	0.006 (0.001) [9] ^a	0.008 (0.001) [6] ^a	0.249 (0.023) [7] ^b
SRP (mg L ⁻¹)	0.008 (0.002) [9] ^a	0.014 (0.001) [7] ^a	0.011 (0.001) [9] ^a	0.027 (0.002) [6] ^b	0.079 (0.006) [7] ^c

Catchment characteristics are based on 1990 data. Physical parameters were measured at the start of each experiment, physicochemical parameters were measured throughout each experiment. Values represent mean (SE). For physical parameters, $n = 10$ at all sites except Suburban ($n = 8$). For physicochemical parameters, numbers in brackets indicate sample size for each value. Letters denote significant differences among sites by Tukey's HSD test for all parameters except shear stress (nonparametric multiple comparisons); sites with the same letter are not statistically different at an overall $\alpha = 0.05$.

n.a., not available (temperature data were not recorded at Agriculture); TSS, total suspended solid; SRP, soluble reactive phosphorus.

*Precipitation data from NOAA's National Climate Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>), station no. 312102 (Forest 1 and Agriculture), station no. 311055 (Forest 2), station no. 310301 (Suburban and Urban).

[†]30-m buffer for 1 km reach upstream of study site.

[‡]Daily maximum temperature.

[§]Daily maximum–daily minimum temperature.

[¶]Deposited sediment on day 40 macroconsumer access tiles at each site (see Methods).

was measured over the centre of each frame with a spherical densiometer (Forest Densimeters, Bartlesville, OK, U.S.A.).

To exclude macroconsumers, one frame in each pair was connected to a 6 V solar-powered fence charger (Parmak Model DF-SP-SS; Parker McCrory Manufacturing Company, Kansas City, MO, U.S.A.) that delivered repeated pulses of electricity ($c. 55 \text{ min}^{-1}$, at a maximum joule rating of 1.4 J) to the 0.25 m² frame area. These electric pulses prevented the entry of crayfish and fish, but did not adversely affect smaller organisms such as aquatic insect larvae. Other researchers have used a similar technique to exclude aquatic insects (e.g. Brown *et al.*, 2000), but exclusion of these smaller organisms requires more powerful chargers and/or shorter distances between electrodes (e.g. 8.4 J across 9 cm in Brown *et al.* (2000), versus 1.4 J across

20 cm in these experiments). Many other studies have excluded only macroconsumers with this electric exclusion technique (e.g. Pringle & Hamazaki, 1998; March *et al.*, 2002), which avoids artifacts associated with traditional cage enclosure/exclosure experiments (e.g. reduced water flow and increased sedimentation).

The spatial extent of the electric field did not vary noticeably across sites, with charges dissipating immediately outside the 0.25 m² frame area at each site. However, conductivity differed across the five sites (range 13–109 µS cm⁻¹), presumably affecting strength of the electric exclusion technique and raising concerns that fish and crayfish may not have been effectively excluded at higher conductivity sites, and that insects (especially larger ones) may have been adversely affected by the exclusion technique at lower conductivity sites. We did not observe any fish or

Table 2 Macroconsumer assemblages at the five study sites

Macroconsumer	Forest 1	Forest 2	Agriculture	Suburban	Urban
Crayfishes					
Species	<i>Cambarus bartonii</i>	<i>Cambarus bartonii</i>	<i>Cambarus bartonii</i>	<i>Cambarus bartonii</i>	<i>Cambarus bartonii</i>
Density* (no. m ⁻²)	2.1	<i>Cambarus robustus</i> 1.6	<i>Cambarus georgiae</i> 1.1	2.2	<i>Cambarus robustus</i> 0.6
Fishes					
Total no. species	6	3	9	11	15
Species†	<i>Cottus bairdii</i> (74)	<i>Cottus bairdii</i> (74)	<i>Cottus bairdii</i> (81)	<i>Campostoma anomalum</i> (76)	<i>Notropis leuciodus</i> (28)
	<i>Clinostomus funduloides</i> Girard (12)	<i>Rhinichthys cataractae</i> (20)	<i>Notropis leuciodus</i> (6)	<i>Lepomis auritus</i> Linnaeus (7)	<i>Luxilus coccogenis</i> (19)
	<i>Oncorhynchus mykiss</i> Walbaum (7)	<i>Rhinichthys atratulus</i> Hermann (6)	<i>Clinostomus funduloides</i> (5)	<i>Hypentilium nigricans</i> Lesueur (5)	<i>Rhinichthys atratulus</i> (19)
	<i>Rhinichthys cataractae</i> Valenciennes (5)				<i>Semotilus atromaculatus</i> (10)
Density* (no. m ⁻²)	0.2	0.2	0.9	1.9	0.7

Crayfish were sampled twice at each site (summer and autumn 1999) using a 1 m² quadrat sampler. Fishes were sampled with a backpack electroshocker (one-pass) at the conclusion of each experiment.

*Total density, all species.

†Only species representing ≥5% total individuals caught are listed; % given in parentheses.

crayfish in exclusion treatments, even at high conductivity sites, and the observed significant differences between access and exclusion treatments at high conductivity sites indicate that macroconsumers were excluded effectively. We found large insects in exclusion treatments at both low and high conductivity sites (e.g. stoneflies at Forest 1, odonates at Urban), and consistently observed greater insect biomass in exclusion versus access treatments.

The unelectrified frame in each pair was accessible to macroconsumers and served as a control, or access treatment. Frames were placed approximately 0.5 m apart to minimize the influence of macroconsumer exclusion treatments on adjacent access treatments. Given that macroconsumers were frequently found immediately outside electrified frames, this distance appeared to be more than adequate. Throughout the experiment, fence charger batteries were replaced every 5 days to ensure a consistent 6 V charge. Frames also were cleared of any accumulated debris every 5 days to minimize flow alterations and prevent loss of frames during spates.

Sampling

Beginning on day 15, one tile was removed from each frame every 5 days. Fence chargers at exclusion

frames were turned off briefly (5–10 min) for sampling. A 210 µm mesh hand net was held downstream of each tile as it was removed to retrieve any dislodged invertebrates or sediment, and tiles were placed in plastic bags and put on ice until they could be processed.

Prior to tile removal each frame was observed for 5 min, and visits by any macroconsumers were recorded. Observation of access and exclusion treatments (total observation time ≥250 min per site) indicated that the exclusion technique effectively excluded fishes and crayfishes at each site. No macroconsumers were observed in exclusion treatments when electrified; macroconsumers occasionally entered when electricity was switched off for sampling, but they left immediately when fence chargers were reactivated. The following macroconsumers were observed in replicates allowing access at each site: five crayfish at Forest 1; 20 sculpins at Forest 2; four sculpins and two crayfish at Agriculture; 14 fish at Suburban and 11 fish at Urban (fish at Suburban and Urban were too small to identify reliably; see Table 2 for fish and crayfish species found at each site).

Tiles were processed within 8 h of sampling. In the laboratory, each tile was rinsed, scraped with a razor blade, and brushed with a nylon toothbrush to

remove invertebrates, algae and sediment. Invertebrates were live-picked under an illuminated magnifier and preserved in 70% ethanol. Given their relatively low abundances at Forest 1, all invertebrates were picked at this site; at the remaining four sites, only large (≥ 4 mm) organisms were picked from whole samples. After invertebrates were removed, the volume of material scraped from each tile was brought to 500 mL and stirred continuously with a magnetic stirrer. In some cases, so much sediment had been deposited on tiles that homogenizing this material was impossible. This bulk sediment (usually coarse sand and gravel) was rinsed and brushed as well as possible, then placed in pans to be dried, weighed and ashed. At Forest 2, Agriculture, Suburban and Urban, small invertebrates were picked from a 100 mL subsample and preserved in 70% ethanol for later identification. A 10 mL subsample was preserved in 2% formalin for algal composition analysis. Equal subsamples (10–100 mL) were filtered onto two pre-ashed $0.45 \mu\text{m}$ glass fibre filters. One filter was used to determine ash-free dry mass (AFDM) and inorganic sediment dry mass, and the other was used for chlorophyll-*a* analysis. Sediment filters were dried for 24 h at 70°C to obtain dry mass, then ashed at 500°C for 1 h and reweighed to obtain AFDM. Bulk sediments underwent a similar process. Total sediments deposited on tiles were then calculated as AFDM + inorganic dry mass (from filters) + bulk sediment dry mass (from pans). Chlorophyll-*a* filters were processed according to standard methods for fluorometric analyses (APHA, 1985), and concentrations were measured with a 10-AU fluorometer (Turner Designs, Sunnyvale, CA, U.S.A.).

Invertebrates were sorted into insects and non-insects. Non-insects were classified as mites, snails, limpets or oligochaetes and counted. Insects were identified to the lowest practical level (usually family or genus; organisms < 1.5 mm were identified to order) with a dissecting microscope ($10\times$ magnification). Individuals were measured to the nearest 0.5 mm with 1 mm grid paper, and biomass was calculated using family-specific length–mass regressions (Benke *et al.*, 1999).

To determine algal species composition, the first 500 cells in a given volume were identified to genus. Biovolume for each taxon was estimated using values available in the literature, and taxa were classified according to growth form as either adnate (e.g.

Achnanthes), motile (e.g. *Navicula*, *Nitzschia*, *Surirella*) or upright (e.g. *Melosira*, *Cymbella*, *Synedra*) (J. Greenwood, pers. comm.).

Statistical analysis

Results presented here are based on data from day 40 at each site, as preliminary analysis indicated that day 40 tiles were representative of patterns seen on earlier sampling dates. Data were analysed via two-factor (site and exclusion) nested (replicate pair nested within site) MANOVAS and ANOVAS. Separate univariate ANOVAS were run for total algal biovolume and total insect biomass; the remaining response variables were grouped as follows in initial MANOVAS: (i) chlorophyll-*a*, AFDM and total sediment; (ii) % algal biovolume contributed by adnate, motile and upright taxa and (iii) biomass of three insect groups common to all sites (Chironomidae, Hydropsychidae, Ephemeroptera), as well as biomass of all other taxa. Across sites, insect assemblages were dominated by Chironomidae, Hydropsychidae and Ephemeroptera; these three groups comprised $> 75\%$ of total insect biomass at each of the five sites. The following families of Ephemeroptera were collected: Heptageniidae (all sites), Baetidae (all sites except Forest 1), Leptophlebiidae (Forest 1), Ephemerellidae (Forest 2, Agriculture and Suburban) and Baetiscidae (Suburban). Taxa comprising the 'other taxa' category also varied among sites (e.g. Perlidae and Perlodidae at Forest 1, Tipulidae at Urban). Non-insect taxa (e.g. snails, limpets and oligochaetes) were collected at all five sites but, in general, abundances tended to be relatively low, especially at less-developed sites; the exception was abundance of Oligochaeta at Urban, which averaged 1630 worms (± 190) m^{-2} in macro-consumer access treatments.

If MANOVAS showed a significant effect ($P < 0.05$), univariate ANOVAS were run for each response variable. Tukey's HSD tests or nonparametric multiple comparison tests were used to assess site-by-site differences (all site-by-site comparisons were based on access treatments at each site). Prior to all statistical analyses, Bartlett's test was used to determine whether variances were equal. All non-proportional data were natural log or natural log + 1 transformed; proportional data were arcsine square-root transformed (Zar, 1999). Unless otherwise noted, $\alpha = 0.05$ for all analyses, and all were performed in SAS[®]

System for Windows™, Release 6.12 (SAS Institute, Cary, NC, U.S.A.).

At Suburban, one replicate pair was excluded from all analyses because the exclusion treatment fence charger did not work properly; thus, there were only four replicate pairs at Suburban rather than five replicate pairs at the other four sites. The only exception to this was insect samples at Forest 2, which also were based on four replicate pairs (one macroconsumer access sample was misplaced). One macroconsumer access replicate at Forest 1 was a significant outlier [Dixon's test (Sokal & Rohlf, 1995); $P < 0.01$] in terms of insect biomass, due to the presence of two large *Pteronarcys* stoneflies with a combined biomass of 7233 mg m^{-2} , compared with a total biomass of all other individuals in that replicate of 303 mg m^{-2} . These two individuals were omitted from all biomass analyses.

To compare the relative effect of exclusion on algal and insect assemblages across sites varying in algal biovolume and insect biomass, we calculated a macroconsumer impact (MI) index, based on the predator impact index in Cooper, Walde & Peckarsky (1990): $MI = -\ln(A/E)$, where A is the response variable value in the macroconsumer access replicate and E is the response value variable in the exclusion replicate. MI indices >0 indicate a positive effect of macroconsumer exclusion (i.e. exclusion increased the response

variable), <0 indicate a negative effect (i.e. exclusion decreased the response variable), and a value of 0 indicates macroconsumers had no effect on the given response variable. MI indices for each variable were compared using one-factor (site) ANOVA.

Results

Macroconsumers significantly affected benthic communities at each site, and responses to macroconsumer exclusion frequently were similar across sites (Table 3). Of the 12 response variables examined, six showed significant effects of exclusion across all sites; only one of these, AFDM, demonstrated a significant site \times exclusion interaction.

Macroconsumer exclusion consistently resulted in significantly higher insect biomass at all sites (Table 3; Fig. 2a). This pattern was due largely to chironomid (Diptera) and hydropsychid (Trichoptera) larvae, as the biomass of both taxa increased when macroconsumers were excluded (Fig. 3a,b; Table 3). Mayfly (most commonly Heptageniidae and Baetidae) larvae were found at all sites, but biomass response to exclusion was variable both within and across sites (Fig. 3c). The responses of other taxa (e.g. predatory stoneflies, tipulids, grazing caddisflies) to exclusion also were variable, and did not show consistent patterns at all sites (Fig. 3d). Usually a specific taxon

Table 3. Results of two-factor (site and exclusion) ANOVAs for insect and algal response variables (all MANOVAs showed significant differences; see Methods)

Response variable	Site		Exclusion		Site \times exclusion	
	F-value [†]	P-value	F-value [‡]	P-value	F-value [†]	P-value
Insects						
Insect biomass	8.78	**	16.90	**	0.40	NS
Chironomids	20.03	***	34.68	***	1.71	NS
Hydropsychids	0.73	NS	4.97	*	0.99	NS
Mayflies	3.55	*	0.52	NS	1.50	NS
Other taxa	1.33	NS	0.43	NS	1.26	NS
Algae						
Chlorophyll- <i>a</i>	91.72	***	32.28	***	2.29	NS
AFDM	10.96	***	31.65	***	6.37	**
Algal biovolume	6.59	**	1.70	NS	2.64	NS
% Adnate taxa	35.66	***	17.74	**	1.46	NS
% Motile taxa	8.96	**	0.21	NS	1.43	NS
% Upright taxa	32.19	***	4.11	NS	1.71	NS

Site refers to differences across five sites representing a range of catchment development; exclusion refers to differences between macroconsumer access and exclusion treatments across all sites.

NS, not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

[†] $F_{4,19}$ for sediment and algal variables, $F_{4,18}$ for insect variables

[‡] $F_{1,19}$ for sediment and algal variables, $F_{1,18}$ for insect variables

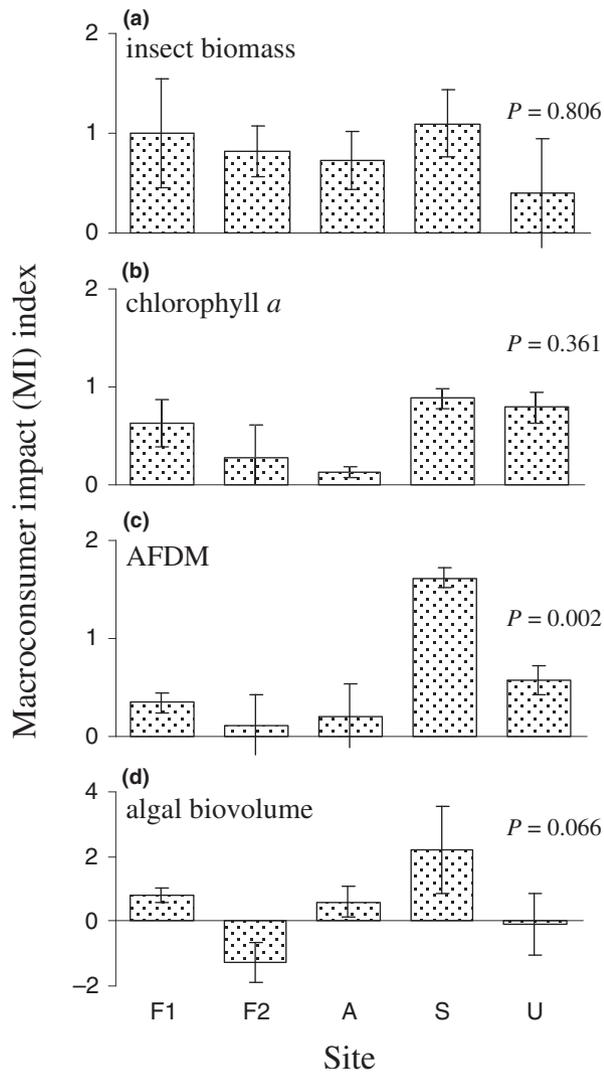


Fig. 2 Macroconsumer impact (MI) index values for (a) total insect biomass, (b) chlorophyll-*a*, (c) AFDM and (d) total algal biovolume at each study site (F1, Forest 1; F2, Forest 2; A, Agriculture; S, Suburban; U, Urban). Positive values indicate that the response variable increased with macroconsumer exclusion, whereas negative values indicate that it decreased. Each bar represents mean of five replicates \pm 1 SE (except for Suburban, where there were four replicates). *P*-values are based on one-way (site) ANOVA for each variable.

in this group of 'others' was not collected at all sites, and thus the responses of these organisms were necessarily more site-specific. For example, predatory stoneflies were common at Forest 1, and showed a significant increase in biomass in exclusion treatments there (Fig. 4d), but were absent from Suburban and Urban.

Across all sites, macroconsumer exclusion resulted in significantly higher chlorophyll-*a* (Table 3). The

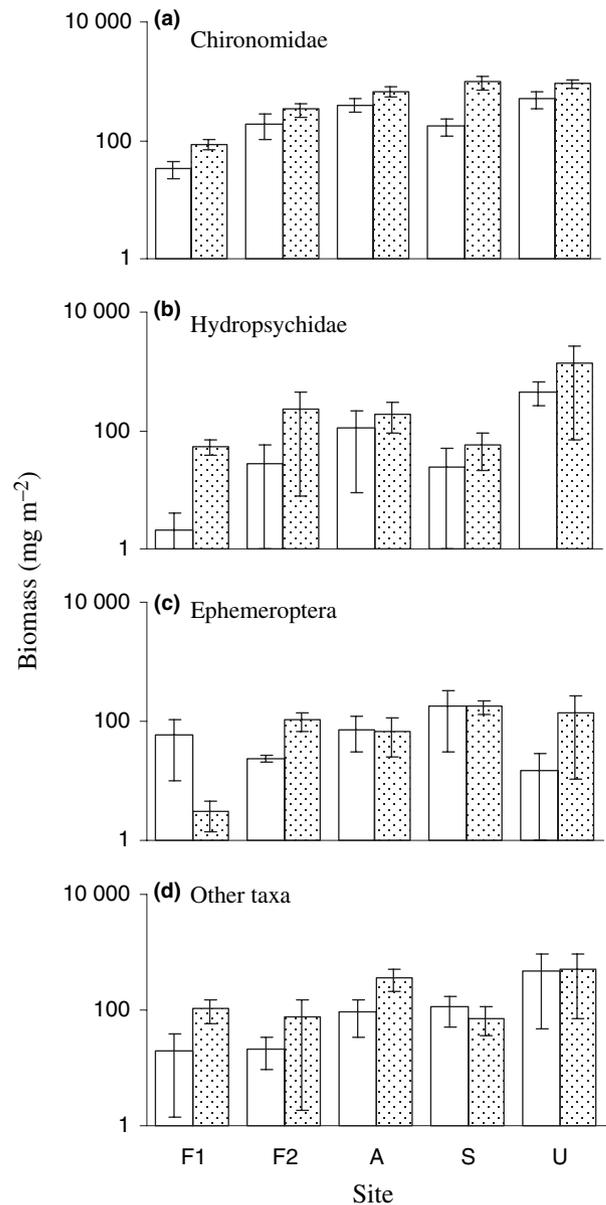


Fig. 3 Biomass of (a) Chironomidae, (b) Hydropsychidae, (c) Ephemeroptera (mayflies) and (d) all other taxa in macroconsumer access (open bars) and exclusion (shaded bars) treatments at each study site (F1, Forest 1; F2, Forest 2; A, Agriculture; S, Suburban; U, Urban). Each bar represents mean of five replicates \pm 1 SE (except for Forest 2 and Suburban, where there were four replicates).

magnitude of this effect was highest at Suburban and lowest at Agriculture; replicate pairs at Forest 2 demonstrated the greatest variability in response (Fig. 2b). In contrast, the effects of exclusion on AFDM were site-specific (Table 3), with exclusion resulting in greater AFDM at some sites (e.g. Suburban and Urban) but not at others (e.g. Forest 2 and

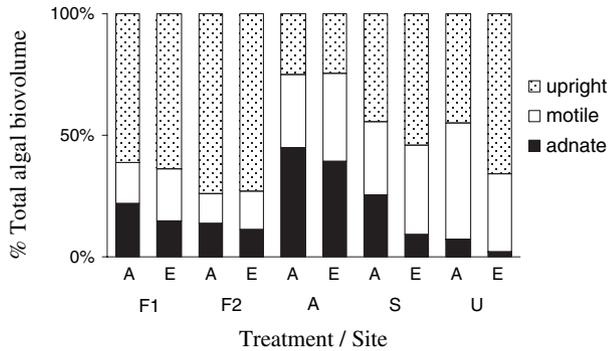


Fig. 4 Percent of total algal biovolume contributed by diatoms representing three physiognomic forms (adnate, motile and upright) in macroconsumer access (A) and exclusion (E) treatments at each site (F1, Forest 1; F2, Forest 2; A, Agriculture; S, Suburban; U, Urban). Each value represents mean of five replicates (except for Suburban, where there were four replicates). Genera classified as adnate include *Achnanthes* and *Achnantheidium*; genera classified as motile include *Navicula*, *Nitzschia* and *Surirella*; genera classified as upright include *Melosira*, *Cymbella* and *Synedra*.

Agriculture; Fig. 2c). A similar pattern was seen for total algal biovolume: biovolume did not show a consistent response to macroconsumer exclusion across all sites, but site-specific responses were nearly significant (site \times exclusion interaction, $P = 0.066$). Macroconsumer exclusion did have a consistent effect on algal composition across all sites; however, adnate diatom taxa (predominantly *Achnanthes* and *Achnantheidium*) comprised a smaller proportion of total biovolume when macroconsumers were excluded, and an increase in the proportion of upright taxa

(e.g. *Synedra*, *Cymbella* and *Melosira*) was nearly significant ($P = 0.057$, Table 3; Fig. 4).

These relatively consistent responses to macroconsumer exclusion were found despite significant differences in the assemblages of insects and algae among the sites. Insect biomass was lowest at Forest 1 and more than an order of magnitude higher at Urban, whereas biomass at the remaining sites showed no clear relationship with catchment development (Table 4). Only hydrosychid biomass and that of taxa other than Hydrosychidae, Chironomidae and Ephemeroptera did not differ significantly across the five sites.

All six algal response variables differed significantly across sites (Table 4). For example, chlorophyll-*a* generally increased with catchment development (although chlorophyll-*a* was relatively high at Forest 2; Table 4), and chlorophyll-*a* was nearly 50 times greater at Urban than at Forest 1. Total algal biovolume was more than 200-fold greater at Urban than at Forest 1; however, algal biovolume at the remaining three sites fell between these two extremes and cross-site differences were not statistically significant (Table 4). The relative proportion of the biovolume attributable to adnate, upright and motile diatoms also differed across sites (Table 4; Fig. 4). For example, biovolume at Forest 1 and Forest 2 was dominated by upright taxa such as *Synedra* and *Cymbella*, while motile taxa (e.g. *Navicula*, *Nitzschia*) were more abundant at sites with greater catchment development (Fig. 4).

Table 4 Insect and algal response variables in access treatments at the five study sites

Response variable	Forest 1	Forest 2	Agriculture	Suburban	Urban
Insects					
Biomass (mg m^{-2})	113 (51) ^a	266 (122) ^{ab}	678 (200) ^b	483 (153) ^{ab}	1460 (493) ^b
Chironomidae	32.9 (10.1)	193 (85.7)	402 (106)	170 (52.3)	507 (164)
Hydrosychidae	2.1 (2.0)	28.3 (28.3)	111 (102)	24.4 (24.4)	450 (190)
Ephemeroptera	58.5 (47.6)	24 (3.3)	74 (45)	176 (145)	14.7 (14.7)
Other taxa	19.7 (18.3)	21.1 (11.8)	91.7 (58.1)	112 (60.7)	490 (441.5)
Algae					
Chlorophyll- <i>a</i> (mg m^{-2})	1.83 (0.44) ^a	24.3 (6.74) ^b	8.54 (0.76) ^c	43.0 (6.53) ^{bd}	89.9 (14.3) ^d
AFDM (g m^{-2})	11.3 (1.81) ^a	21.2 (4.69) ^{ab}	19.5 (5.94) ^{ab}	17.9 (7.23) ^{ab}	46.6 (10.2) ^b
Biovolume ($\mu\text{m}^3 \text{cm}^{-2} \times 10^5$)	48.4 (12.2) ^a	858 (351) ^{ab}	606 (377) ^{ab}	1325 (1030) ^{ab}	9768 (5925) ^b

Each value represents the mean of five replicates (1 SE) for day-40 data (except for Suburban, where there were four replicates). Letters denote significant differences among sites by Tukey's HSD test; sites with the same letter are not statistically different at an overall $\alpha = 0.05$. Tukey's tests were not carried out for individual taxa due to unequal variances across sites.

Discussion

Changes in macroconsumer assemblages associated with landscape development did not significantly alter the outcome of top-down interactions. Despite cross-site differences in physical, chemical and biological characteristics, responses to macroconsumer exclusion were remarkably consistent, with macroconsumers affecting total insect biomass, biomass of common insect taxa, chlorophyll-*a* and algal composition similarly across five sites varying in catchment perturbation. These findings suggest functional redundancy exists across different macroconsumer assemblages, with specialist feeders (i.e. fish classified as obligate benthic invertivores) at less developed sites being replaced functionally by more generalist feeders (i.e. fish classified as algivores and general invertivores) at more developed sites (Ledger & Hildrew, 2005).

We expected changes in macroconsumer assemblage composition and other site characteristics (e.g. sedimentation) to diminish top-down control of benthic insects at sites with more developed catchments; contrary to our prediction, total insect biomass increased whenever macroconsumers were excluded, largely due to increased biomass of Chironomidae and Hydropsychidae larvae. Given that the relative strength of top-down forces may be weaker near the base of the food web (e.g. McQueen, Post & Mills, 1986; Forrester, Dudley & Grimm, 1999), it is perhaps more surprising that the response of certain algae to exclusion also was relatively consistent among sites. As predicted, algal responses (e.g. AFDM, total biovolume) to macroconsumer exclusion were more variable than insect responses. However, across all sites, macroconsumers reduced chlorophyll-*a* and affected algal composition by increasing the proportion of adnate (e.g. *Achnanthes*) and decreasing the proportion of upright and filamentous diatoms (e.g. *Melosira*, *Cymbella*). Adnate taxa tend to be more grazer-resistant, and thus fared well in treatments allowing access by macroconsumers (Lamberti *et al.*, 1989; Feminella & Hawkins, 1995); when macroconsumers were excluded, more grazer-susceptible upright taxa were able to increase, despite concomitant increases in insect biomass. Crayfish were common at all sites and, though they often are considered primarily to be detritivores (Schofield *et al.*, 2001; Evans-White, Dodds & Whiles, 2003), it

is likely that they significantly affected algal assemblages by direct grazing (Charlebois & Lamberti, 1996; Evans-White *et al.*, 2003).

Although these findings suggest functional redundancy of different macroconsumer assemblages associated with catchment development, it should be kept in mind that top-down effects on insects and algae are very narrow measures of function (Rosenfeld, 2002). Our findings do not suggest that macroconsumers at these sites were functionally equivalent — rather, that specific end results of consumer effects were similar. Despite the functional redundancy of macroconsumers in terms of reducing total insect biomass and biomass of common insect taxa, consumers at individual sites also had site-specific effects, such as the reduction of predatory stonefly biomass at Forest 1. Most insect taxa (with the exception of Chironomidae, Hydropsychidae and various Ephemeroptera families) were not collected at all sites and, even at individual sites, many taxa were collected in only one or a few replicates. Thus, the responses of these localized taxa were necessarily site-specific. It also is possible that the pathways leading to reduced insect biomass at each site may have differed. Our experimental design did not allow us to separate trophic from non-trophic interactions, so macroconsumers at some sites may have affected biotic communities directly via consumption, while macroconsumers at other sites affected these communities indirectly via incidental dislodgement or alteration of habitat.

In addition, the environments in which these macroconsumers were acting differed considerably across the five sites, and this environmental context can significantly influence redundancy (Wellnitz & Poff, 2001). We were not comparing the effects of different macroconsumers in similar environments. Thus, the expected decreases in top-down effects in perturbed systems, given different macroconsumer faunas, may have been offset by numerous other changes associated with development, including: (i) increased susceptibility to top-down effects of pollution-tolerant, relatively sedentary insects such as Chironomidae and Hydropsychidae larvae; (ii) increased predation efficiency of macroconsumers on embedded substrata with few refugia for prey (e.g. Brusven & Rose, 1981) and (iii) decreased availability of terrestrial insects due to alteration of riparian vegetation (e.g. Nakano, Miyasaka & Kuhara, 1999). As a result, generalist fishes may have had similar

effects on benthic insects in human-modified streams as obligate benthic insectivores in relatively unaltered systems. Increased productivity due to light and nutrient subsidies may have further enhanced consumer effects (e.g. Oksanen *et al.*, 1981; Wellnitz & Ward, 1998).

Physical, chemical and biological differences across the five study sites were similar to those in many other studies of human impacts on streams; our sites were thus typical of streams in developed catchments. For example, nutrient concentrations, water temperature, conductivity and sediment generally increase with development, while canopy cover typically decreases (Allan, 2004; Walsh *et al.*, 2005). Relatively tolerant invertebrates, such as larval Chironomidae, larval Hydropsychidae and Oligochaeta, tend to dominate as development increases (Paul & Meyer, 2001; Allan, 2004; Walsh *et al.*, 2005), and sediment-tolerant diatoms (i.e. motile taxa such as *Navicula*, *Nitzschia* and *Surirella*) comprise a greater proportion of the algal biovolume (Kutka & Richards, 1996; Munn, Black & Gruber, 2002). Fish species richness may actually increase with catchment land use change (Scott & Helfman, 2001), but fish assemblages can shift from predatory species feeding on the stream bottom (e.g. mottled sculpin) at forested sites to algivorous or more generalist cyprinids in perturbed systems (Schlosser, 1982; Harding *et al.*, 1998; Jones *et al.*, 1999; Burcher & Benfield, 2006).

This range of cross-site differences highlights one of the challenges inherent in examining how land use alterations affect biotic interactions *in situ*: many factors likely to influence these interactions are altered simultaneously, and these changes may have contradictory effects. For example, increased light and nutrients may increase primary productivity and ultimately strengthen top-down effects (Oksanen *et al.*, 1981; Wellnitz & Ward, 1998). In our streams, biotic communities were apparently stimulated by agricultural activity and development, as response variables such as chlorophyll-*a* and insect biomass were greater at more perturbed sites (Paul & Meyer, 2001; Taylor *et al.*, 2004; Busse, Simpson & Cooper, 2006). However, increased algal biovolume and insect biomass did not contribute to stronger macroconsumer effects at sites impacted by human activity.

Conversely, factors such as increased sedimentation (Peckarsky, 1985; Schofield *et al.*, 2004) and shifts to less benthic macroconsumers (Dahl & Greenberg,

1996; Gido & Matthews, 2001) may diminish top-down effects on the benthos. Thus, the net effects of land use change on ecosystems ultimately depend on the relative importance of anthropogenic influences that strengthen consumer control, compared with those that diminish it. By experimentally examining top-down effects in systems subject to these numerous and potentially competing influences, we were able to examine the net impact on biotic interactions of changes typical in developed systems.

In conclusion, macroconsumers had remarkably consistent effects on stream benthic communities across five sites representing a range of catchment development, and their influence on insects and algae was not eliminated by in-stream changes associated with human development. Although many studies have examined the direct effects of catchment development and associated in-stream changes on stream communities, few have considered the repercussions of these changes for species interactions (McDonnell & Pickett, 1990; Paul & Meyer, 2001). Given the potential importance of top-down interactions in determining ecosystem structure and function, and the prevalence of landscape alteration, further examination of these issues will greatly improve our understanding of trophic dynamics and biotic interactions in a world increasingly modified by humans.

Acknowledgments

This research was supported by NSF grant DEB-96-32854 to the Coweeta LTER site. Thanks to K. Kearns, S. Pohlman, A. Ramírez and M. Scott for their help with field and lab work; J.B. Wallace for temperature data and J. Greenwood and T. Clason for algal composition analysis. Special thanks are extended to the Asheville Country Club and Patterson Oil Company, who generously allowed us access to our study reaches, and to R. and C. Chapman, who provided us a home (and a makeshift lab) for the summer. The Pringle lab group, K. Kearns, M. Freeman, C. Jennings, J.B. Wallace and two anonymous reviewers provided insightful comments on earlier versions of the manuscript.

References

- Allan J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics*, **35**, 257–284.

- APHA [American Public Health Association] (1985) *Standard Methods for Examination of Water and Wastewater*, 16th edn. American Public Health Association, Washington, D.C.
- Benke A.C., Hurny A.D., Smock L.A. & Wallace J.B. (1999) Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, **18**, 308–343.
- Bolstad P.V. & Swank W.T. (1997) Cumulative impacts of land use on water quality in a southern Appalachian watershed. *Journal of the American Water Resources Association*, **33**, 519–533.
- Brown G.G., Norris R.H., Maher W.A. & Thomas K. (2000) Use of electricity to inhibit macroinvertebrate grazing of epilithon in experimental treatments in flowing waters. *Journal of the North American Benthological Society*, **19**, 176–185.
- Brusven M.A. & Rose S.T. (1981) Influence of substrate composition and suspended sediment on insect predation by the torrent sculpin, *Cottus rhotheus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1444–1448.
- Burcher C.L. & Benfield E.F. (2006) Physical and biological responses of streams to suburbanization of historically agricultural watersheds. *Journal of the North American Benthological Society*, **25**, 356–369.
- Busse L.B., Simpson J.C. & Cooper S.D. (2006) Relationships among nutrients, algae, and land use in urbanized southern California streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2621–2638.
- Charlebois P.M. & Lamberti G.A. (1996) Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society*, **15**, 551–563.
- Cooper J.E. & Braswell A.L. (1995) Observations on North Carolina crayfishes (Decapoda: Cambaridae). *Brimleyana*, **22**, 87–132.
- Cooper S.D., Walde S.J. & Peckarsky B.L. (1990) Prey exchange rates and the impact of predators on prey populations in streams. *Ecology*, **71**, 1503–1514.
- Dahl J. & Greenberg L. (1996) Impact on stream benthic prey by benthic vs. drift feeding predators: a meta-analysis. *Oikos*, **77**, 177–181.
- Dunson W.A. & Travis J. (1991) The role of abiotic factors in community organization. *The American Naturalist*, **138**, 1067–1091.
- Evans-White M.A., Dodds W.K. & Whiles M.R. (2003) Ecosystem significance of crayfishes and stonerollers in a prairie stream: functional differences between co-occurring omnivores. *Journal of the North American Benthological Society*, **22**, 423–441.
- Feminella J.W. & Hawkins C.P. (1995) Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society*, **14**, 465–509.
- Forrester G.E., Dudley T.L. & Grimm N.B. (1999) Trophic interactions in open systems: effects of predators and nutrients on stream food chains. *Limnology and Oceanography*, **44**, 1187–1197.
- Gido K.B. & Matthews W.J. (2001) Ecosystem effects of water column minnows in experimental streams. *Oecologia*, **126**, 247–253.
- Harding J.S., Benfield E.F., Bolstad P.V., Helfman G.S. & Jones E.B.D. III (1998) Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences*, **95**, 14843–14847.
- Hunter M.D. & Price P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural environments. *Ecology*, **73**, 724–732.
- Jones E.B.D. III, Helfman G.S., Harper J.O. & Bolstad P.V. (1999) Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology*, **13**, 1454–1465.
- Kutka F.J. & Richards C. (1996) Relating diatom assemblage structure to stream habitat quality. *Journal of the North American Benthological Society*, **15**, 469–480.
- Lamberti G.A., Gregory S.V., Ashkenas L.R., Steinman A.D. & McIntire C.D. (1989) Productive capacity of periphyton as a determinant of plant–herbivore interactions in streams. *Ecology*, **70**, 1840–1856.
- Ledger M.E. & Hildrew A.G. (2005) The ecology of acidification and recovery: changes in herbivore–algal food web linkages across a stream pH gradient. *Environmental Pollution*, **137**, 103–118.
- March J.G., Pringle C.M., Townsend M.J. & Wilson A.I. (2002) Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. *Freshwater Biology*, **47**, 377–390.
- McDonnell M.J. & Pickett S.T.A. (1990) Ecosystem structure and function along urban – rural gradients: an unexploited opportunity for ecology. *Ecology*, **71**, 1232–1237.
- McKinney M.L. (2002) Urbanization, biodiversity, and conservation. *BioScience*, **52**, 883–890.
- McQueen D.J., Post J.R. & Mills E.L. (1986) Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1571–1581.
- Munn M.D., Black R.W. & Gruber S.J. (2002) Response of benthic algae to environmental gradients in an agriculturally dominated landscape. *Journal of the North American Benthological Society*, **21**, 221–237.
- Nakano S., Miyasaka H. & Kuhara N. (1999) Terrestrial–aquatic linkages: riparian arthropod inputs alter

- trophic cascades in a stream food web. *Ecology*, **80**, 2435–2441.
- Oksanen L., Fretwell S.D., Arruda J. & Niemela P. (1981) Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, **118**, 240–261.
- Paul M.J. & Meyer J.L. (2001) Streams in the urban landscape. *Annual Review of Ecology and Systematics*, **32**, 333–365.
- Peckarsky B.L. (1985) Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology*, **63**, 1519–1530.
- Pringle C.M. & Hamazaki T. (1998) The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology*, **79**, 269–280.
- Rosenfeld J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–162.
- SAMAB [Southern Appalachian Man and the Biosphere] (1996) *The Southern Appalachian Assessment Social/Cultural/Economic Technical Report*, Report 4 of 5. U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, GA.
- Schlosser I.J. (1982) Trophic structure, reproductive success, and growth rate of fishes in a natural and modified headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 968–978.
- Schofield K.A., Pringle C.M., Meyer J.L. & Sutherland A.B. (2001) The importance of crayfish in the breakdown of rhododendron leaf litter. *Freshwater Biology*, **46**, 1191–1204.
- Schofield K.A., Pringle C.M. & Meyer J.L. (2004) Effects of increased bedload on algal and detrital-based stream food webs: experimental manipulation of sediment and macroconsumers. *Limnology and Oceanography*, **49**, 900–909.
- Scott M.C. (2006) Winner and losers among stream fishes in relation to land use legacies and urban development in the southeastern US. *Biological Conservation*, **127**, 301–309.
- Scott M.C. & Helfman G.S. (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, **26**, 6–15.
- Sokal R.R. & Rohlf F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman and Company, New York, NY.
- Statzner B. & Müller R. (1989) Standard hemispheres as indicators of flow characteristics in lotic benthos research. *Freshwater Biology*, **21**, 445–459.
- Sutherland A.B., Meyer J.L. & Gardner E.P. (2002) Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology*, **47**, 1791–1805.
- Taylor S.L., Roberts S.C., Walsh C.J. & Hatt B.E. (2004) Catchment urbanisation and increased benthic algal biomass in streams: linking mechanisms to management. *Freshwater Biology*, **49**, 835–851.
- Walker B.H. (1992) Biodiversity and functional redundancy. *Conservation Biology*, **6**, 18–23.
- Walsh C.J., Roy A.H., Feminella J.W., Cottingham P.D., Groffman P.M. & Morgan R.P. II (2005) The urban stream syndrome: current knowledge and the search for a cure. *Journal of the North American Benthological Society*, **24**, 706–723.
- Wellnitz T.A. & Poff N.L. (2001) Functional redundancy in heterogeneous environments: implications for conservation. *Ecology Letters*, **4**, 177–179.
- Wellnitz T.A. & Ward J.V. (1998) Does light intensity modify the effect mayfly grazers have on periphyton? *Freshwater Biology*, **39**, 135–149.
- Zar J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ.

(Manuscript accepted 8 July 2008)