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Terrestrial organic matter as subsidies that aid in the recovery of macroinvertebrates in industrially damaged lakes

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Abstract. The importance of allochthonous carbon to the productivity of stream ecosystems in temperate ecozones is well understood, but this relationship is less established in oligotrophic lakes. The nearshore littoral zones, at the interface of terrestrial and aquatic systems, are areas where the influence of terrestrial subsidies is likely greatest. We investigated the response of nearshore communities to variation in the quantity and composition of allochthonous materials, determined the landscape characteristics that regulate the variation of this subsidy, and explored the potential for terrestrial restoration practices to influence the export of organic matter to lakes. Stepwise multiple regressions revealed that diversity of nearshore macroinvertebrate families increased with the amount of fine particulate organic matter (FPOM) captured in sediment traps. The quantity of FPOM (g) increased with forest cover, and the relative amount of FPOM (percentage of total particulate material) in the traps increased with surface area of wetland in the catchments. These models suggest that terrestrially derived subsidies are important in smelter-impacted watersheds, and that the restoration of forests and wetlands will speed the return of nearshore consumer community diversity in industrially damaged lakes.

Key words: benthic macroinvertebrates; decomposition; diversity; industrial damage; littoral zones; mining; organic matter; recovery; restoration; trophic subsidies.

Introduction

The flow of energy in pelagic food webs is more complex than suggested by the traditional phytoplankton-driven model. The role of allochthonous sources of carbon in structuring lake food webs has recently been emerging (reviewed by Reynolds 2008). At the margin of lakes strong trophic linkages between terrestrial and aquatic habitats occur that are crucial for sustaining both littoral and pelagic food webs (Schindler et al. 1996, Vanni et al. 2005, Prairie 2008). The flow of organic material derived from terrestrial sources can support benthic macroinvertebrates upon which fishes rely (France 1995), and can even directly support some fish populations (Goulding 1980, Nakano et al. 1999, Mehner et al. 2005, Vanni et al. 2005). These inputs of organic matter amount to a trophic subsidy to consumer communities in aquatic systems. While the relationship between allochthonous organic matter and macroinvertebrates has been extensively studied in streams (e.g., Hall et al. 2000), this relationship is poorly understood in lakes. To what degree are nearshore benthic macroinvertebrate communities dependent on allochthonous organic matter, and what characteristics of the landscape regulate the exports of this organic matter?

Questions about the role of terrestrial inputs can best be answered in systems that vary broadly in these trophic subsidies, and the lakes around Sudbury, Ontario offer just this unique opportunity. These lakes and their watersheds have suffered a century of acidification and metal contamination from the large mining and smelting industries in the region. However, major reductions (approximately 90%) in atmospheric emissions of pollutants have led to widespread water quality improvements in recent decades and substantial recolonization of fish, zooplankton, and other aquatic biota has been observed (Keller et al. 1999, 2007). Unfortunately damage to the terrestrial ecosystems remains severe. Forests were devastated by the long period of intensive ground level fumigation and the resulting soil erosion created vast areas of near barren land. With improved air quality some revegetation has occurred, but little organic material exists in the soils and the flow of organic matter to lakes may be severely reduced (SARA Group 2009). In some watersheds, remedial liming of damaged soils hastened vegetation recovery, but much of this liming was limited to corridors along roadways and other visible areas, with the aim of improving aesthetics not restoring ecosystems (Winterhalder et al. 2001, Gunn et al. 2007). The result is a patchwork of watersheds with very different degrees of vegetative recovery.

We took advantage of this gradient in terrestrial recovery to determine the follow-on effects on lake

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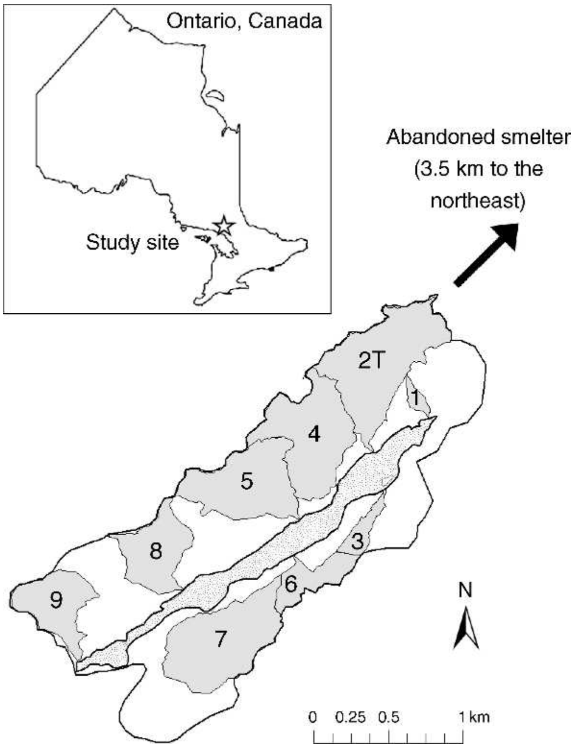


FIG. 1. Daisy Lake watershed (46°27′ N, 80°52′ W) near the Coniston Smelter in Sudbury, Ontario, Canada. The smelter is located 3.5 km to northeast of the lake. It was abandoned in 1972. The nine study catchments used in this study (2–39 ha) are shown and labeled. Catchment 2T was used in an experimental liming project in the mid 1990s.

littoral systems. We studied the effects of varying inputs of terrestrial organic matter on benthic macroinvertebrates and decomposition in the nearshore areas of industrially damaged lakes. The goal of this study was to investigate the response of nearshore communities to variation in the quantity and composition of allochthonous materials, determine the landscape characteristics that regulate the variation of this subsidy, and explore the potential of terrestrial restoration procedures to increase the export of this material to lakes.

METHODS

Study area and design

The Daisy Lake watershed (275 ha; see Plate 1) is located 3.5 km southwest of the abandoned Coniston Smelter near Sudbury, Canada, and consists of 13 small catchments (2–39 ha) that discharge through intermittent streams into a 36-ha lake (14.0 m maximum depth; Fig. 1). The lake was very acidic (pH < 5.0) and metal contaminated in the 1980s ([Cu] > 0.071 mg/L, [Ni] > 0.305 mg/L), but with closure of the nearby smelter and major emission reductions in other operating smelters (Keller et al. 2003) acidity and metal concentrations in the lake declined rapidly (Fig. 2). The forest too was heavily impacted, and is displaying slow recovery. Paleolimnological studies revealed that the original pine (*Pinus* spp.) and spruce (*Picea* spp.) dominated forest was lost in the 1940s and the barren watershed experienced heavy soil erosion (Dixit et al. 1996). Large areas of exposed bedrock remain today but recolonization of trees and shrubs is occurring in valleys and other areas with residual soil layers. The forest around Daisy Lake now consists mainly of white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and a few other less abundant species.

We selected nine of the 16 Daisy Lake catchment areas that varied most widely in forest cover. These are numbered from 1 to 9 in order of closest (1) to farthest (9) from the smelter as measured at the discharge point of the stream into the lake. The second closest catchment to the smelter had been used as a treatment site for a watershed restoration experiment in the mid 1990s, and is identified as treated (2T). In 1994, 410 tons of coarse dolomitic limestone (53.9% $CaCO_3$, 44.8% $MgCO_3$) were aerially applied across the entire catchment, and an additional 54 tons of fine pelletized dolomite (54.5% $CaCO_3$, 45.0% $MgCO_3$) were applied to the wetlands in 1995 (Gunn et al. 2001). Two years later, the catchment was fertilized and seeded with five species of grasses and two species of legumes, the typical seed mix used in the Sudbury reclamation program (Gunn et al. 2001, Winterhalder et al. 2001).

Landscape characteristics of the nine catchments

We surveyed each catchment in two different ways. For the entire catchment, the overall characteristics of the forest communities were assessed through interpretation of aerial photographs. The borders of each catchment were delineated from 1:2000 scale (2-m contour) maps. The surface area (proportional cover as well as total area) of wetland, forest, and semi-barren rock was measured from 1:40 000 aerial photographs taken July 2003. The second method was a detailed ground-level forest survey that was conducted within a 100 m radius immediately surrounding the mouth of

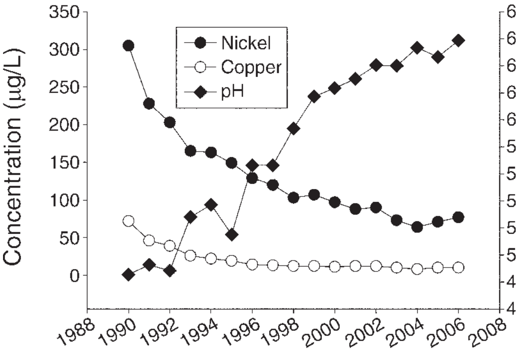


FIG. 2. Temporal trends in pH, Ni, and Cu concentration in Daisy Lake. Values in 2006 are 6.59, 77.4 μg/L, and 9.6 μg/L, respectively. Data are from the Ontario Ministry of the Environment and the Cooperative Freshwater Ecology Unit, Sudbury, Ontario.

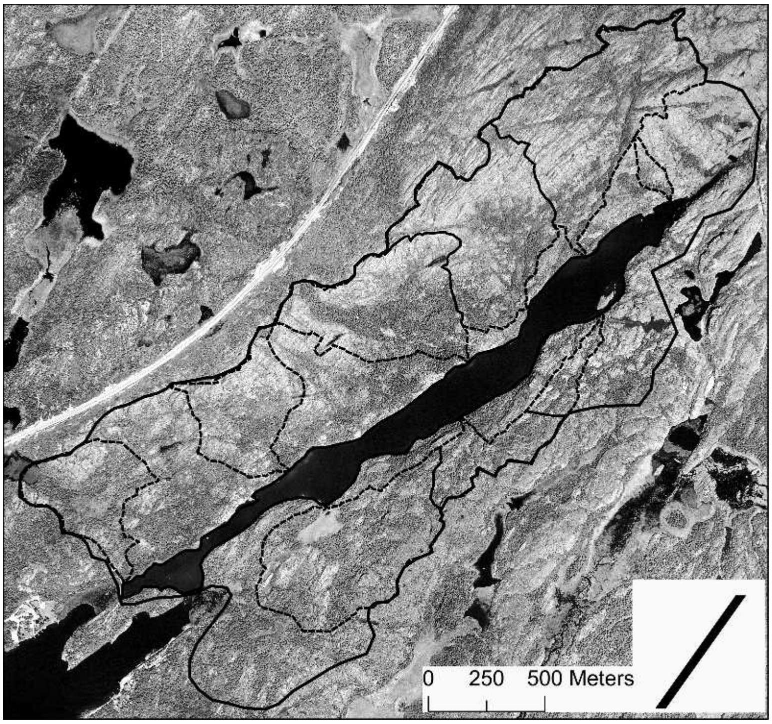


PLATE 1. Aerial photograph (1:40 000) of the Daisy Lake watershed taken in July 2003 (Ortho Imagery of the City of Greater Sudbury). The contrast of vegetation cover (dark) and barren rock (light) is evident across the watershed. The nine study catchments are outlined within the watershed boundary. Photo credit: Greater Sudbury, Ontario (Canada) city database.

each catchment's discharge stream. We defined this area as the riparian zone of each catchment. ArcGIS 9.2 software (Environmental Systems Research Institute, Redlands California, USA) was used to randomly select sampling points spaced at least 8 m apart, and the points were navigated with a handheld GPS unit. At each survey point a forestry prism was used to determine basal area (m^2/ha), and all trees that were large enough to meet the inclusion criteria of prism refraction techniques were measured for diameter at breast height (dbh). Humic layer thickness was measured from a soil core and percent canopy cover was determined using a spherical densiometer. Soil samples were collected at three sites in the riparian area, dried, filtered through a 1-mm sieve, and sent to the University of Joensuu, Finland, for determination of metal and base cation concentrations.

Catchment drainage water and exported organic matter

Water samples were collected one or two days after rain events, with six or seven samples collected during the ice-free seasons of 2007 and 2008. Samples were taken from an appropriate location within 15 m upstream of the point where water entered the lake, and were sent to the Ontario Ministry of the Environment in Dorset, Ontario for analysis (as outlined in Ontario Ministry of the Environment 1983).

Twelve 50-mL polypropylene centrifuge tubes (3 cm diameter × 10 cm height) were deployed in the lake at each discharge location to collect particulate material. These sediment traps were held upright in the holes of standard construction bricks placed close to the mouths of the streams at depths between 0.15 m and 0.5 m, and left for five weeks (October–November 2007). The samples were rinsed through a 250-µm sieve to separate fine and coarse components. Fine particulate material was homogenized with a magnetic stirrer and subsampled (approximately 10%) before vacuum filtration through 1.5-µm pre-combusted and pre-weighed filter paper. Samples of both coarse material and fine material were oven dried at 60°C for two days and then combusted at 500°C for two hours. Mass loss after combustion was used as a measure of the organic component of the samples. Masses of fine particulate organic matter (FPOM), coarse particulate organic matter (CPOM), fine particulate inorganic matter (FPIM), and coarse particulate inorganic matter (CPIM) were averaged across replicates to generate representative values for each catchment. Proportions of both fine and coarse organic material in the traps were also calculated.

Deltas

The nearshore sites below each catchment were defined as the area of sediment deposition, or the delta, at the stream–lake interface (ranging in size from 33.5 m^2 to 704.0 m^2). Five equally spaced transects were set up on the deltas, extending as rays from the stream

TABLE 1. Landscape characteristics of nine Daisy Lake catchments.

	Entire catchment				Riparian forest			
Catchment	Surface area (ha)	Semi-barren area (%)	Wetland area (%)	Forest area (%)	Tree diameter (mm)	Canopy cover (%)	Basal area (m^2/ha)	Soil humic layer (mm)
1	1.97	74.62	0.0	25.38	65.9 ± 30.7	30.9 ± 25.3	2.5 ± 4.1	13.3 ± 13.6
2T	39.36	68.06	1.22	30.72	69.8 ± 36.5	69.0 ± 19.9	9.9 ± 6.9	61.2 ± 54.8
3	4.49	56.57	4.23	39.20	79.4 ± 43.7	36.0 ± 27.4	4.3 ± 5.5	33.0 ± 46.7
4	32.29	68.29	1.30	30.41	83.0 ± 61.3	17.0 ± 25.1	2.7 ± 4.5	26.2 ± 55.2
5	29.13	50.08	1.92	48.0	116.3 ± 60.0	64.3 ± 22.7	10.6 ± 7.3	24.3 ± 16.5
6	10.09	39.15	0.0	60.85	100.4 ± 65.0	45.6 ± 36.5	4.8 ± 5.3	32.0 ± 43.6
7	34.31	38.50	6.32	55.17	104.3 ± 66.9	27.0 ± 32.9	3.3 ± 4.6	15.2 ± 18.9
8	18.39	59.82	0.0	40.18	144.2 ± 63.4	51.6 ± 29.0	7.1 ± 7.4	34.0 ± 25.8
9	17.16	35.66	9.38	54.95	91.7 ± 51.6	58.9 ± 24.7	5.5 ± 4.9	43.2 ± 20.9

Notes: Area of semi-barren rock, forest, and wetland were determined from interpretation of 2003 aerial photographs. Means ± SD are displayed for forest stand measures from 30 random sites in the riparian zones (100 m from shore). Catchment 2T is a treated catchment, limed in 1994 and 1995, fertilized and seeded in 1997.

discharge point to the inflection point where the area of sediment deposition began to drop off into deep water. Point-transect surveys were conducted by snorkeling along transects and recording the presence or absence of woody debris and macrophytes at 0.40-m intervals. The proportion of points with woody debris and macropyhtes was used to estimate the extent of each substrate at the deltas.

Macroinvertebrate diversity and leaf litter breakdown

Coarse-mesh leaf packs were constructed of 5.0-mm mesh material, and smaller fine-mesh leaf packs were constructed of 0.5-mm mesh material. The coarse-mesh packs were filled with white birch leaves collected the previous fall from a site unaffected by smelter effluent. The leaves were left in a tub of flowing water for two days to allow initial leaching to occur, dried, and then weighed to approximately 4 g per pack. The fine-mesh leaf packs were filled with 10, 15 mm diameter white birch leaf pieces collected and pre-leached in the same manner. Six coarse-mesh leaf packs and six fine-mesh leaf packs were pre-weighed and then placed on the deltas at the mouths of each stream inside the holes of standard 20 cm concrete blocks set parallel to shore.

The leaf packs and sediment traps were deployed during the time of natural leaf fall (October to November 2007). The concrete blocks helped to minimize wave, wind, and sunlight exposure differences across sites by providing shelter, and simultaneously preventing sediment burial of the leaf packs. Distance of the leaf packs from the stream inflows varied with delta morphology. Instead of a using a fixed lateral distance, the concrete blocks were placed at the closest distance to the inflow where the sediment traps and leaf packs would be fully submerged (0.15–0.50 m depth). After six weeks, the coarse-mesh leaf packs were removed, preserved in 5% formalin and dyed with Phloxine B to aid in the separation of macroinvertebrates from debris. The fine-mesh leaf packs were preserved in 2% formalin.

In the laboratory, the coarse-mesh leaf packs were rinsed and the large leaf pieces cleaned and separated. The leaf pieces were dried at 60°C for two days, and weighed to quantify loss of mass. The leaf pieces in the fine-mesh leaf packs were cleaned, dried, and weighed in the same manner. The material captured on a 250-μm sieve was sorted under a microscope for identification of macroinvertebrates.

A second method of estimating diversity, the kick-and-sweep method, was also used. These two methods likely differ in their ability to collect certain types of organisms, and so this complement of methods allowed for the detection of various patterns that exist in relation to landscape characteristics. Two weeks after removing the leaf packs, three 10-minute kick-and-sweep samples were collected at each delta using a 500-μm mesh sweep net. Materials collected in each replicate sample were homogenized and a 1-L subsample was preserved in 10% formalin for two days before transferring to 70% ethanol. At least 100 macroinvertebrates were collected for identification from each replicate using a Marchant box random subsampling method (Marchant 1989). All macroinvertebrates (except Nematoda, Oligochaeta, Coelenterata, and Hydracarina) from both collection methods were identified to family level. Abundances of taxa were averaged across replicates for each delta and several common metrics of community composition and feeding-group types were calculated. Regression modeling was restricted to the Simpson diversity index, as it varied most widely across the deltas.

Statistical analyses

Multiple regressions were used to explore the relationships between landscape characteristics, exported organic matter, and nearshore macroinvertebrate communities. Drainage water chemistry, and the presence of woody debris and macrophytes on the deltas were included in the models. Principal components analysis (PCA) was used to reduce chemistry measures to varimax rotated components. The 17 stream chemistry variables used in the models included pH, dissolved organic carbon (DOC), and several cations, nutrients, and metals (Al, Ba, Ca, Cu, Fe, Mg, Mn, N, Na, Ni, P, K, Si, Sr). Stream water, soil, and forest measurements were log(x) or log($x + 1$) transformed and all propor-

TABLE 2. Selected stream water quality characteristics of nine catchments of Daisy Lake.

Catchment	pH	DOC (mg/L)	Ca (mg/L)	Mg (mg/L)	K (mg/L)	Na (mg/L)	Al (μg/L)
1	4.65 ± 0.03	0.90 ± 0.33	1.33 ± 0.24	0.62 ± 0.10	0.28 ± 0.06	1.21 ± 0.16	787 ± 54
2T	6.79 ± 0.41	4.61 ± 1.29	3.51 ± 0.62	2.69 ± 0.65	0.32 ± 0.10	0.87 ± 0.14	92 ± 36
3	6.18 ± 0.06	5.20 ± 1.48	2.51 ± 0.45	1.27 ± 0.21	0.31 ± 0.05	1.47 ± 0.15	144 ± 44
4	4.70 ± 0.10	3.67 ± 1.91	1.35 ± 0.64	0.75 ± 0.38	0.31 ± 0.24	1.15 ± 0.19	306 ± 116
5	6.04 ± 0.10	3.05 ± 1.38	2.24 ± 0.41	0.99 ± 0.19	0.42 ± 0.36	1.61 ± 0.16	102 ± 35
6	6.00 ± 0.21	4.05 ± 1.22	2.17 ± 0.56	1.13 ± 0.27	0.38 ± 0.17	1.33 ± 0.12	116 ± 36
7	6.51 ± 0.11	11.18 ± 1.42	4.51 ± 3.15	2.27 ± 1.47	0.22 ± 0.16	1.91 ± 0.61	127 ± 42
8	4.93 ± 0.20	1.83 ± 0.58	1.56 ± 0.28	0.76 ± 0.10	0.31 ± 0.03	1.61 ± 0.22	260 ± 56
9	5.01 ± 0.15	3.43 ± 0.84	1.46 ± 0.36	0.70 ± 0.18	0.28 ± 0.09	2.30 ± 1.16	203 ± 29

Notes: Values are means ± SD ($n = 6$ or 7). DOC stands for dissolved organic carbon. Catchment 2T is a treated catchment, limed in 1994 and 1995, fertilized and seeded in 1997.

tions were arcsine $[\sqrt{(x)}]$ transformed. PCA sample scores were averaged to generate a catchment value and then used as predictors in regression modeling. The use of PCA scores as predictors in multiple regression is a method employed to minimize multicollinearity among independent variables while retaining the full set of measurements for interpretation (Graham 2003). Any remaining colinear pairs of independent variables were investigated with pair-wise correlation and the one most strongly correlated to the response variable was kept in the analysis.

Multiple linear regressions were used to explain the variance in macroinvertebrate community composition in relation to stream water chemistry and organic matter. The stepwise method was used to select variables for the most parsimonious model, with a probability of F criteria of <0.10 for entry and >0.15 for removal. Regressions were repeated for Simpson diversity on leaf packs, Simpson diversity in kick-and-sweep surveys, mass loss of coarse-mesh leaf packs, and mass loss of fine-mesh leaf packs. The variables that explained most of the variance in community composition were then used as dependent variables in subsequent multiple linear regressions to relate these exported subsidies to specific landscape characteristics.

As an additional investigation, Mann-Whitney U tests were used to compare the percentage of macroinvertebrate shredders in Daisy Lake to proportions found in both kick-and-sweep samples from catchment streams in a less impacted watershed (Nelson Lake) that lies ~30 km to the north of Sudbury, and samples from 20 circumneutral lakes located near Dorset, Ontario (250 km east; data are from the Cooperative Freshwater Ecology Unit, collected in 2005).

RESULTS

Landscape characteristics of the catchments

GIS mapping revealed that forest cover varied from 25.4% to 60.9% and was lowest in catchment 1. Wetland cover varied from 0% to 9.4% and was highest in catchment 9 and 7 (9.4% and 6.3%, respectively; Table 1). Considerable variation in the nearshore or riparian forest conditions was also detected across catchments. Mean basal area ranged from 2.5 m^2/ha to 10.6 m^2/ha among the catchments, and canopy cover ranged from 17.0% to 69.0%. Catchment 7 had a distinctive riparian area dominated by a large wetland and a very narrow band of trees near the stream mouth, resulting in low riparian basal area (3.3 m^2/ha) and canopy cover (27.0%). Catchments 5 and 2T had relatively dense stands, with high mean basal areas (10.6 m^2/ha and 9.9 m^2/ha) and canopy cover (64.3% and 69.0%; Table 1). The metal concentrations in soils were generally high but varied greatly across the catchments. Cu ranged from 0.07 to 0.92 g/kg and was highest in catchment 4. Ni in

TABLE 3. Leaf litter mass loss (from $n = 6$ leaf packs); coarse and fine particulate organic matter (CPOM, FPOM) and inorganic matter (CPIM, FPIM) quantities from sediment traps ($n = 12$); and macrophyte and woody debris cover for each delta nine catchments of Daisy Lake.

Catchment	Coarse-mesh leaf pack mass loss (%)	Fine-mesh leaf pack mass loss (%)	FPOM (g)	FPIM (g)	CPOM (g)	CPIM (g)
1	28.60 ± 3.12	29.94 ± 0.75	0.05 ± 0.02	0.66 ± 0.22	0.28 ± 0.17	1.86 ± 0.97
2T	33.76 ± 5.89	31.54 ± 3.06	0.11 ± 0.02	1.02 ± 0.18	0.73 ± 0.09	6.92 ± 3.76
3	31.41 ± 1.57	31.49 ± 2.67	0.03 ± 0.01	0.15 ± 0.05	0.27 ± 0.02	0.60 ± 0.10
4	31.93 ± 2.70	30.87 ± 1.82	0.05 ± 0.02	0.07 ± 0.02	0.23 ± 0.08	0.11 ± 0.02
5	34.69 ± 1.51	27.67 ± 5.26	0.11 ± 0.02	1.83 ± 0.50	0.60 ± 0.15	3.14 ± 0.71
6	33.59 ± 1.17	31.97 ± 3.87	0.03 ± 0.01	0.13 ± 0.03	0.15 ± 0.05	0.47 ± 0.25
7	33.75 ± 2.47	33.48 ± 2.15	0.08 ± 0.03	0.14 ± 0.04	0.24 ± 0.17	0.17 ± 0.11
8	32.77 ± 2.24	33.32 ± 0.65	0.05 ± 0.02	0.27 ± 0.10	0.15 ± 0.09	0.26 ± 0.12
9	32.55 ± 1.24	30.09 ± 4.44	0.07 ± 0.07	0.26 ± 0.33	0.02 ± 0.02	0.03 ± 0.02

Notes: Means ± SD are shown. Catchment 2T is a treated catchment, limed in 1994 and 1995, fertilized and seeded in 1997.

Table 2. Extended.

Cu (μg/L)	Fe (μg/L)	Mn (μg/L)	Ni (μg/L)
52 ± 3	56 ± 62	106 ± 14	190 ± 107
21 ± 5	32 ± 27	2 ± 2	148 ± 119
30 ± 4	43 ± 21	2 ± 1	197 ± 56
34 ± 14	362 ± 616	118 ± 80	181 ± 90
13 ± 4	119 ± 75	17 ± 10	143 ± 63
21 ± 4	30 ± 23	4 ± 3	231 ± 131
33 ± 11	383 ± 376	11 ± 10	469 ± 390
11 ± 2	23 ± 17	86 ± 13	148 ± 80
15 ± 2	55 ± 44	74 ± 19	131 ± 36

these soils ranged from 0.02 to 0.45 g/kg and was highest in catchments 4 and 2T.

Catchment drainage water

Dissolved organic carbon (DOC) in stream water varied widely among catchments, from 0.90 mg/L to 11.18 mg/L and was highest at one of the wetland-dominated catchments (7). Stream water pH ranged from 4.65 to 6.79 (highest at 2T), and Al concentration was highest in catchment 1 (787 μg/L), which also had the lowest stream water pH (Table 2). The amount of exported particulate matter was highest from the treated catchment (2T) and catchment 5. Catchment 5 had the highest mean FPOM and FPIM in the sediment traps (0.11 g and 1.83 g, respectively), while 2T had the highest discharged CPOM and CPIM (0.73 g and 6.92 g, respectively; Table 3).

Nearshore macroinvertebrate communities

There were 32 taxa of macroinvertebrates in the deltas of Daisy Lake's catchments, with 14 filter feeders, 12 predators, two scrapers, one group of parasites, and three families of leaf shredders (Table 4). Diversity of benthic macroinvertebrate families varied greatly along the deltas. The mean Simpson diversity index ranged from 0.051 to 0.641 on the leaf packs, and 0.070 to 0.579 in the kick-and-sweep samples (Table 4). Principal components analysis confirmed that strong diversity gradients occurred along Daisy Lake, and revealed that these gradients represented shifts away from filter-feeder organisms towards leaf shredders and predators (Fig. 3). Diversity in both the kick-and-sweep and the leaf-pack samples closely followed FPOM (g) and FPOM percent, respectively, across the nine catchments (Fig. 4). Daisy Lake had a significantly lower percentage of shredders than were found below the Nelson Lake catchments (Mann-Whitney $U = 1.000$, $P < 0.001$) and in the Dorset reference lakes (Mann-Whitney $U = 0.000$, $P < 0.001$; Fig. 5).

Table 3. Extended.

FPOM (%)	CPOM (%)	Macrophyte cover (%)	Woody debris cover (%)
1.76 ± 0.50	9.40 ± 2.48	21.1	0.00
1.36 ± 0.46	9.30 ± 2.98	53.9	8.86
3.00 ± 0.72	25.66 ± 2.26	45.3	12.86
11.12 ± 1.99	49.21 ± 4.87	45.8	17.74
1.91 ± 0.18	10.58 ± 1.34	68.9	12.89
3.90 ± 0.88	19.43 ± 2.53	42.1	11.54
14.48 ± 4.77	33.55 ± 9.61	71.2	15.65
7.27 ± 1.80	19.11 ± 5.19	82.3	9.67
19.77 ± 3.51	6.25 ± 2.52	90.0	5.74

Leaf litter breakdown

Breakdown of leaf litter (measured as percent mass loss) varied across catchments with a mean mass loss in the large mesh leaf packs ranging from a low of 28.6% and 31.4% at the catchments closest to the smelter (1 and 3 respectively) to 34.7% at catchment 5 (catchment with well-treed valley). A Fisher LSD test revealed that percent mass loss was significantly higher at site 5 than sites 1 and 3 (one-way ANOVA $F_{8,45} = 2.481$, $P = 0.025$). Mean mass loss in the fine mesh leaf packs varied from 27.7% at catchment 5 to 33.5% at catchment 7, but these differences were not significant (one-way ANOVA $F_{8,44} = 2.004$, $P = 0.068$; Table 3).

Multiple regression models:
Diversity and leaf litter breakdown

The 17 stream water chemistry variables were reduced to four significant principal components. Water PC 1 explained 37.7% of the variance and was positively loaded (0.75 or higher) by pH, DOC, Mg, and Ca and negatively loaded by Ba and Mn. Mean Water PC 1 scores were highest at the treated catchment (2T) and catchments 7 and 3, and lowest at the catchment 4. Water PC 2 explained an additional 20.8% of the variance and was positively loaded (0.75 or higher) by Ni, and had the highest mean score at catchment 7. Water PC 3 explained an additional 14.1% of the variance and was negatively loaded (0.75 or higher) by Cu and also had the highest mean score at catchment 7.

Stepwise multiple regressions revealed that increases in macroinvertebrate diversity across the nine catchments were related to increases in FPOM. The quantity of discharged FPOM (g) was positively related to increases in diversity of families in the kick-and-sweep samples, explaining almost 40% of the variation in Simpson diversity index (stepwise multiple regression $F_{1,7} = 6.111$, $P = 0.043$, adjusted $R^2 = 0.390$). Simpson diversity of families on the leaf packs increased with increasing proportion of FPOM (%) ($P = 0.002$, R^2 change $= 0.499$), increasing amount of FPOM (g) ($P = 0.040$, R^2 change $=$ 0.256), decreasing Water PC 3 ($P = 0.030$, R^2 change $=$ 0.126), and increasing Water PC 1 ($P = 0.075$, R^2 change $=$ 0.068). All variables together explained almost 90% of the variation in diversity of the leaf packs (stepwise multiple regression $F_{4,4} = 18.697$, $P = 0.007$, adjusted $R^2 = 0.898$; Table 5).

Leaf litter breakdown (percent mass loss) in the coarse-mesh leaf packs increased with Water PC1 ($P =$

TABLE 4. Metrics of community composition of macroinvertebrates found on the deltas of nine catchments in Daisy Lake by kick-and-sweep and leaf-pack sampling.

Catchment	Simpson diversity index	Shredders (%)	Collectors (%)	Predators (%)	Scrapers (%)
Leaf packs					
1	0.051 ± 0.04	0	85.3 ± 4.2	1.0 ± 1.6	0.5 ± 1.1
2T	0.530 ± 0.07	0	70.6 ± 3.8	5.6 ± 3.6	2.4 ± 3.9
3	0.161 ± 0.04	0	79.1 ± 4.0	4.7 ± 2.8	0
4	0.569 ± 0.15	1.1 ± 2.7	53.6 ± 11.2	12.6 ± 8.7	0
5	0.262 ± 0.03	0	78.2 ± 3.9	2.7 ± 2.2	0
6	0.249 ± 0.05	0	85.9 ± 3.7	2.0 ± 2.2	0
7	0.641 ± 0.07	4.8 ± 1.2	63.0 ± 4.2	8.6 ± 1.5	14.0 ± 6.0
8	0.305 ± 0.15	0	77.5 ± 3.6	7.8 ± 2.9	1.1 ± 2.8
9	0.588 ± 0.09	1.7 ± 2.7	64.5 ± 4.4	23.5 ± 4.4	2.3 ± 2.6
Kick and sweep					
1	0.070 ± 0.03	0	84.2 ± 5.2	5.8 ± 5.2	0
2T	0.579 ± 0.12	0	64.8 ± 5.2	25.2 ± 5.2	0
3	0.267 ± 0.13	0	81.2 ± 4.4	8.8 ± 4.4	0
4	0.291 ± 0.12	0	73.9 ± 2.3	16.1 ± 2.3	0
5	0.388 ± 0.12	3.3 ± 5.7	78.1 ± 3.4	10.4 ± 3.9	0
6	0.209 ± 0.03	0	83.2 ± 5.9	5.7 ± 5.0	3.6 ± 3.2
7	0.244 ± 0.08	0	83.9 ± 1.3	6.1 ± 1.3	0
8	0.104 ± 0.03	1.9 ± 3.2	83.2 ± 1.6	6.1 ± 1.3	0
9	0.431 ± 0.12	3.0 ± 2.7	70.7 ± 6.0	18.9 ± 5.7	0

Notes: Metrics are calculated at the family level of identification, and means ± SD are displayed ($n = 3$ for kick and sweep, $n = 6$ for leaf packs). Shredders include Limnephilidae, Phryganeidae, and Pyralidae. Scrapers include Heptageniidae and Hydroptilidae. Collectors include Caenidae, Chironomidae, Corixidae, Entomobryidae, Hypogastruridae, Isotomidae, Leptoceridae, Leptophlebiidae, Oligochaeta, Poduridae, Polycentropodidae, Scirtidae, Coelenterata, and Tipulidae. Predators include Aeshnidae, Belostomatidae, Certatopogonidae, Chaoboridae, Coenagrionidae, Corduliidae, Dytiscidae, Empididae, Gyrinidae, Hydracarina, Libellulidae, and Tabanidae.

0.025, R^2 change = 0.552) and macrophyte cover on the deltas ($P = 0.080$, R^2 change = 0.191) together explaining over 60% of the variation in breakdown (stepwise multiple regression $F_{2,6} = 8.654$, $P = 0.017$, adjusted $R^2 = 0.657$). Breakdown (percent mass loss) in fine-mesh leaf packs increased with decreasing FPIM, with over 40% of the variation in breakdown explained (stepwise multiple regression $F_{1,7} = 7.228$, $P = 0.031$, adjusted $R^2 = 0.438$; Table 5).

Multiple regression models: Fine particulate matter

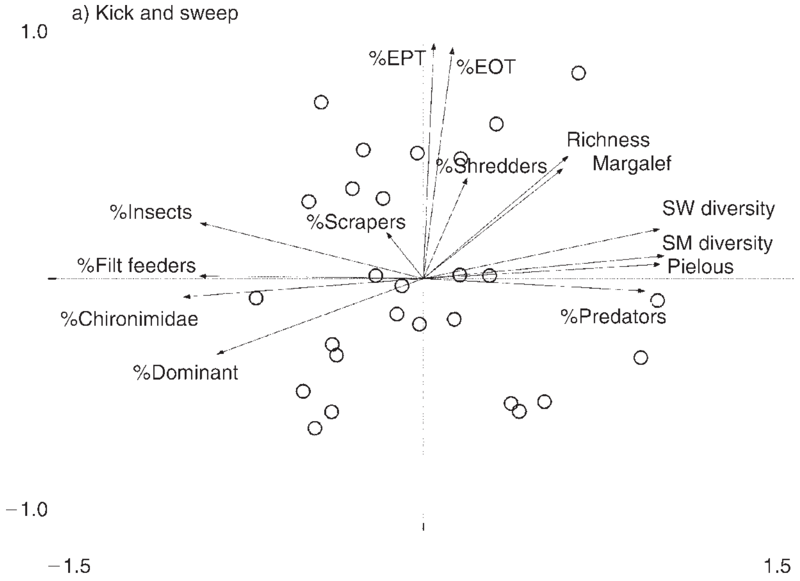
The eight soil chemistry variables were reduced to two significant principal components. Soil PC 1 explained 62.2% of the variance and was positively loaded (0.75 or higher) by Mg, Ca, Mn, and Zn. Catchments 7, 6, and 2T had the highest mean soil PC 1 scores. Soil PC 2 explained an additional 17.5% of the variance and was positively loaded (0.75 or higher) by Ni and Cu. Catchments closest to the smelter (1, 2T, 3, 4) had the highest mean Soil PC 2 scores.

The amount of FPOM increased with absolute forest area (m^2; $P = 0.040$, R^2 change = 0.525) in the catchment and with mean basal area in the riparian forest ($P = 0.072$, R^2 change = 0.210). Together they explained almost 65% of the variation in amount of FPOM (g) (stepwise multiple regression $F_{2,6} = 8.321$, $P = 0.019$, adjusted $R^2 = 0.647$). The mean basal area in the riparian forest was also positively related to amount of discharged FPIM (g), explaining more than 40% of the variation (stepwise multiple regression $F_{1,7} = 6.824$, $P = 0.035$, adjusted $R^2 = 0.421$; Table 5).

Catchments with higher wetland area (m^2) exported a higher amount of particulate material to the deltas. This single variable explained more than 40% of the variation in proportion of FPOM ($F_{1,7} = 7.310$, $P = 0.030$, adjusted $R^2 = 0.441$; Table 5).

DISCUSSION

Our results suggest that FPOM deposition in the nearshore areas (deltas) is primarily of allochthonous (terrestrial) origin, and that amount of this deposited material varies across the deltas. Forests and wetlands represent organic matter islands in these barren landscapes, and their effects on receiving waters are evident in the large deltas found only at stream discharge points. There appears to be little organic matter in nearshore areas away from the stream deltas. Although it is likely that some of the material collected in the sediment traps was resuspended, we found strong positive correlations between the export of FPOM and landscape characteristics. The sediment exported from wetland-dominated catchments appeared to be of a higher quality (in terms of FPOM %) than inputs from upland catchments. Wetlands seemed to act as "collection sites," where water, coarse material, and inorganic matter was trapped with more fine particulates or dissolved fractions being exported to receiving waters.


a) Kick and sweep

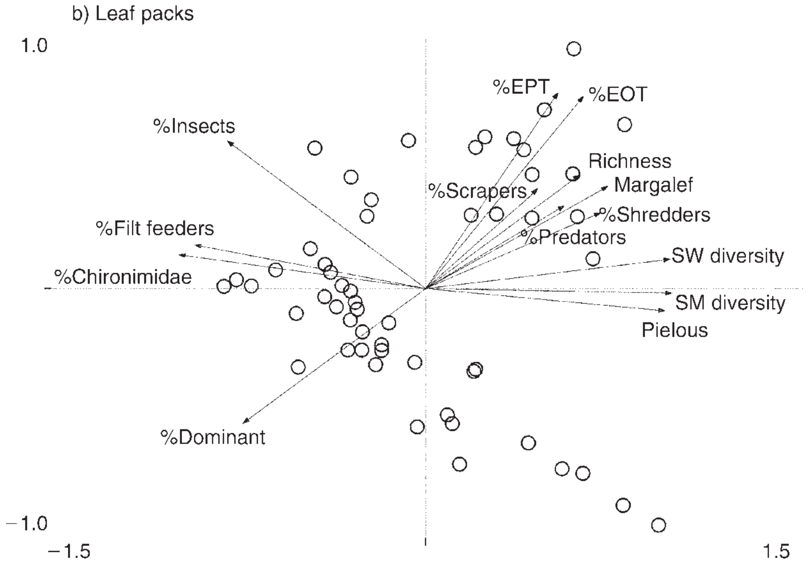

b) Leaf packs

FIG. 3. Principal-components biplot showing community composition metrics and feeding groups (arrows) across two axes for (a) three replicates of kick-and-sweep samples and (b) six replicates of leaf-pack replicates in nine nearshore delta sites of Daisy Lake. Circles represent individual replicates across each site. Metrics of community composition include Richness, SW diversity (Shannon Wiener diversity), SM diversity (Simpson diversity), Pielous (evenness), Margalef (richness), %EOT (% Ephemeroptera, Odonata, and Trichoptera), %EPT (% Ephemeroptera, Plecoptera, Trichoptera), %Insects, %Chironimidae, and %Dominant (proportion of most dominant taxa). Feeding groups are %Shredders, %Scrapers, %Predators, and %Filt feeders (filter feeders).

Others have reported that short term disturbances, such as wildfire or logging, increase the export of particulate organic matter as a result of soil erosion and organic debris from the forest floor (e.g., Carignan and Steedman 2000). However, when the recovery of terrestrial vegetation is delayed over many decades, as is the case in Sudbury, soil erosion continues and the resulting areas of barren bedrock offers little opportunity for vegetation to reestablish (SARA Group 2009). Cores from Daisy Lake reveal a dramatic spike in sedimentation in the mid 1900s, followed by a rapid decline in exported material (Dixit et al. 1996). The observed correlations between forest/wetland cover and export of organic material suggest that it is reduced by the delayed recovery of vegetation, and likely the associated return of organic soils. It appears that the

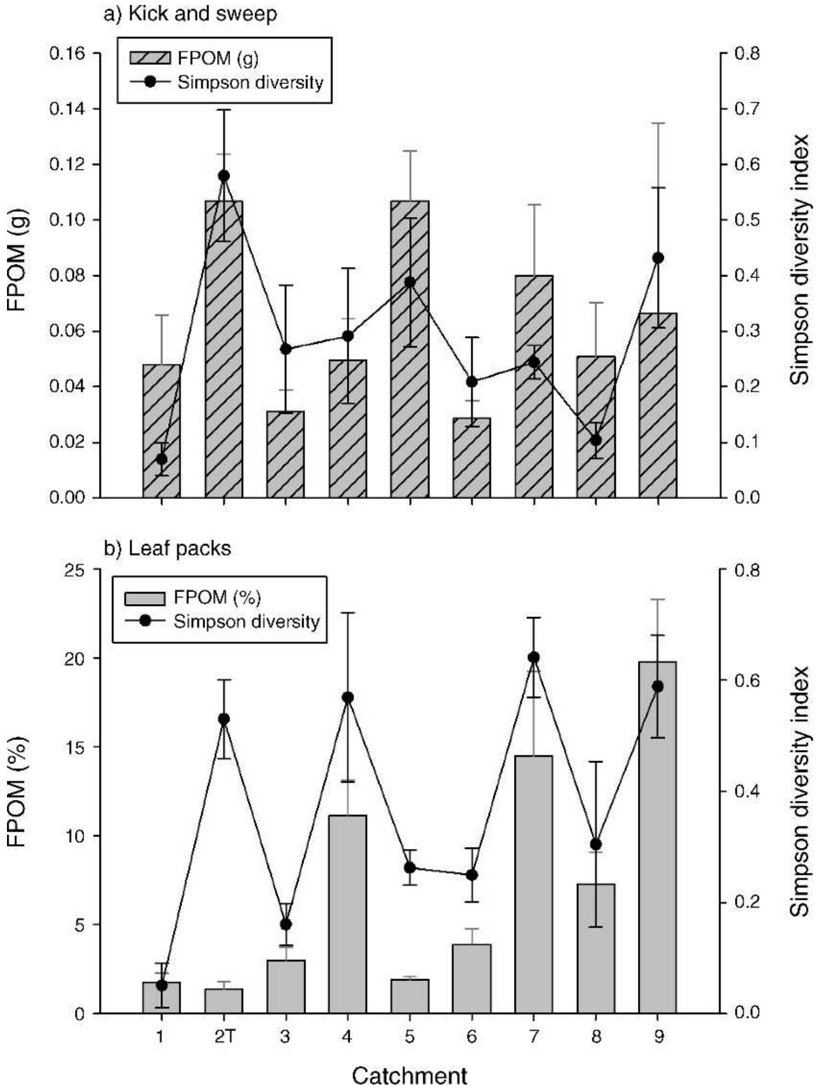


FIG. 4. Simpson diversity index (mean ± SD) in (a) kick-and-sweep samples ($n = 3$) and (b) leaf-pack samples ($n = 6$) closely tracks fine particulate organic matter (FPOM) mass (g) and FPOM as a percentage of the sample from $n = 12$ sediment traps, respectively, across nine delta sites in Daisy Lake.

rebuilding of soil and organic debris through forest succession and restoration, as well as wetland rehabilitation is needed to enhance the export of organic material to the nearshore areas of lakes.

Allochthonous FPOM is an important trophic subsidy, and reductions in this subsidy had negative impacts on consumers of organic matter. The diversity of macroinvertebrates increased with both the proportional (%) and absolute amount (g) of FPOM in the sediment traps, and FPOM was directly related to the condition of the catchment. The influence of metals, nutrients, pH, and other stream chemistry measures on benthic macroinvertebrates were small in comparison to the influence of the organic matter subsidy. In particular, the consumer communities found in deltas that were associated with wetland-influenced catchments were the most diverse and also had the highest abundance of benthic organisms in the nearshore areas, related to an increased proportional amount of this subsidy in particulate exports. Resource availability, diversity, and productivity have been found to be closely related in terrestrial and aquatic systems and across a variety of taxa (Naeem et al. 1994, Duffy et al. 2005, Cardinale et al. 2006). Theories of this interaction have included the influence of resource availability on diversity through increased abundance within populations and reductions in extinction rates, and inversely the effect of increased diversity on productivity through more efficient use of resources (reviewed by Cardinale et al. 2009). Any subsidy thus has the potential to have an influence on diversity or productivity, and potentially both.

The increase in nearshore consumer diversity caused by allochthonous FPOM also has the potential to influence the functioning of the entire lake food web. Many fishes, including some species that roam the pelagic zone also feed on littoral benthos thus coupling the nearshore community to the larger lake food web (Schindler et al. 1996, Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002). Foraging fishes rely on a diversity of macroinvertebrate species and families with a range of body size as they grow and shift their diet from smaller to larger prey (Boisclair and Leglett 1989, Rasmussen et al. 2008). In our study, increases in macroinvertebrate family diversity were generally associated with increases in larger-bodied predator families, presumably because FPOM acts as a food source for their consumer prey. Larger-bodied macroinvertebrates are preferred food items for fishes (Persson 1987). Population surveys have shown that the fish community in Daisy Lake is stunted (Cooperative Freshwater Ecology Unit, *unpublished data*) and this reduction of suitable benthic food may be a cause. Indeed, low availability of benthic invertebrates appears to be affecting the growth of fish in several Sudbury area lakes (Luek et al. 2010). The strength of the benthic subsidy thus has the potential to affect trophic levels far removed from the terrestrial source. In our study, leaf shredders (generally larger-bodied taxa) were particularly low in diversity and relative abundance in Daisy Lake compared to nearby reference systems. This may be the result of a lack of nearby colonist sources, residual metal levels, the return of these sensitive taxa, differences in predation pressure between lakes, and/or a limited supply of coarse organic matter on which they rely. The lack of larger-bodied macroinvertebrates has the potential to reduce the growth and population size of fishes (Rasmussen et al. 2008, Luek et al. 2010).

In addition to a paucity of leaf shredders, microbial decomposition of organic matter appeared to be slowed by a heavy accumulation of inorganic erosional material on leaf surfaces. Microbial communities appear to be responsible for most of the in-lake leaf litter decomposition, as the average mass loss in the fine-mesh leaf packs at each site was almost identical to that measured in the coarse-mesh leaf packs. The only site that had a large deviation from this ratio was the site where the highest amount of fine inorganic material was found. It was observed that the litter packs were heavily coated with this inorganic material. This coating was examined with scanning electron imagery and was found to be an ochre, an inorganic iron oxide compound commonly associated with acid mine drainage (Cooperative Freshwater Ecology Unit, *unpublished data*). Siefert and Mutz (2001) noted a reduction in leaf litter breakdown with the presence of such ochre. The precipitation of terrestrial solutes as acidic drainage water from still-impacted landscapes entering circumneutral lake water may be a persistent problem in such sites. Land restoration practices will not only encourage the production of organic matter subsidies, but may also reduce the deposition of this ochre, and encourage decomposition.

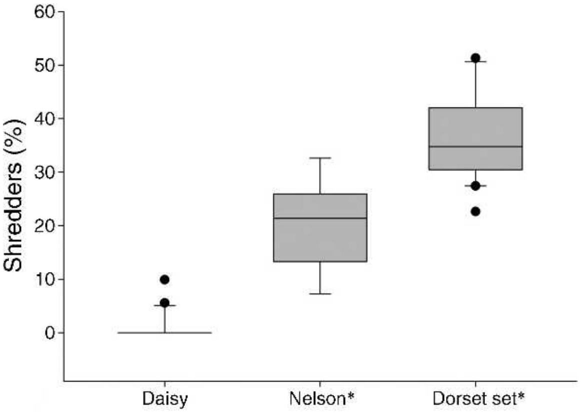


FIG. 5. Proportion of leaf shredders in kick-and-sweep samples from Daisy Lake and Nelson Lake in comparison to a set of circumneutral reference lakes in Dorset, Ontario (250 km from Sudbury). The boundaries of the box indicate 25th and 75th percentiles, the line within the box is the median, the error bars are 10th and 90th percentiles, and outliers are indicated with a dot. There is very little variation around the median of Daisy Lake data, with 23 of 27 values equaling 0, which is why the quartiles are not all visible. Significant differences ($P < 0.05$) from Daisy Lake (Mann-Whitney *U* tests) are indicated with an asterisk.

Land reclamation has the potential to improve in-lake primary productivity as well. Reduction of acidity through liming has been shown to hasten the recovery of macrophytes in softwater lakes (Brouwer and Bobbink 2002). Restoration practices (e.g., land liming) that increase stream water pH and the export of nutrients, and also decrease metal concentrations, may stimulate the growth of macrophytes and other primary producers in the nearshore areas. Pelagic primary production can also be enhanced through the transfer of nutrients from littoral to pelagic food webs by water movement and foraging fishes (Schindler et al. 1996, Vanni and de Ruiter 1996, Vanni et al. 2005). Differences in the nutrient content of organic matter subsidies across these sites with varying forest and wetland cover warrants further investigation.

In this study, the artificial leaf packs acted much like natural leaf litter accumulations that trap and hold fine organic matter (Richardson 1992). Larger woody debris also traps organic matter and promotes increases in macroinvertebrate biomass (Rasmussen and Rowan 1997, Pabst et al. 2008). The presence of coarse woody debris in littoral zones of healthy lakes is of course related to the amount of woody debris in the associated riparian zone. In our severely impacted watershed, leaf litter and woody debris was very scarce across most deltas. Natural recovery and replanting of riparian forests should release not just more leaves but also more coarse woody debris into lakes and this may help trap

TABLE 5. Summary of stepwise regression models, showing intercept, standardized slope, test values, and r^2 for all predictor variables that significantly entered the models.

Model and variables	Beta	t	F	df	P	Partial and total r^2	Adjusted R^2
Fine-mesh mass loss (%)							
Intercept		53.052			<0.001		
FPIM	−0.713	−2.689	7.228	1, 7	0.031	0.508	0.438
Course-mesh mass loss (%)							
Intercept		28.361			<0.001		
Water PC1	0.633	2.965			0.025	0.552	
Macrophytes (%)	0.450	2.108			0.080	0.191	
Total			8.654	2, 6	0.017	0.743	0.657
Simpson diversity index (kick and sweep)							
Intercept		0.499			0.633		
FPOM (g)	0.683	2.472	6.111	1, 7	0.043	0.466	0.390
Simpson diversity index (leaf packs)							
Intercept		−2.889			0.045		
FPOM (%)	1.069	7.626			0.002	0.499	
FPOM (g)	0.381	3.008			0.040	0.256	
Water PC3	−0.453	−3.300			0.030	0.126	
Water PC1	0.309	2.394			0.075	0.068	
Total			18.697	4, 4	0.007	0.949	0.898
FPOM (g)							
Intercept		0.037			0.972		
Forest area	0.576	2.608			0.040	0.525	
Riparian forest basal area	0.481	2.178			0.072	0.210	
Total			8.321	2, 6	0.019	0.735	0.647
FPIM (g)							
Intercept		−1.292			0.237		
Riparian forest basal area	0.703	2.612	6.824	1, 7	0.035	0.494	0.421
FPOM (%)							
Intercept		4.390			0.003		
Wetland area	0.715	2.704	7.310	1, 7	0.030	0.511	0.441

and hold FPOM and other subsidies in the nearshore areas. Well-treed riparian zones may also enhance the amount of terrestrial insect material that enters lakes. All of these measures would promote nearshore benthic macroinvertebrate diversity and reestablish a more normal level of benthic support for limnetic food webs.

With the recent recognition that both allochthonous carbon sources and the processing of organic matter in nearshore areas plays a major role in pelagic food webs, the important connection between terrestrial and aquatic systems is becoming more apparent. These connections should be considered in the application of restoration procedures for all ecosystems. This study shows that forests and wetlands promote macroinvertebrate diversity and function through the subsidy of fine particulate organic matter. If the spatial variation in recovery state is thought of as a surrogate measure of temporal variation, then the recovery of lake communities must await recovery on land, and terrestrial restoration has the potential to hasten this process. Not only will the restoration of forests and wetlands promote the export of this trophic subsidy, but riparian forest restoration can also increase the supply of coarse woody debris and leaf litter to nearshore areas, enhancing the retention of the material. When liming is used as a restoration technique, the associated improvements in stream chemistry may reduce ochre precipitation and influence nearshore communities through the stimulation of macrophyte regrowth and promotion of primary production. It is recommended that land restoration programs target stressed watersheds to encourage the development of organic soils in barren uplands, enhance tree growth in riparian areas, and restore wetlands to promoting the return of biodiversity and ecosystem function to terrestrial and aquatic systems simultaneously.

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LITERATURE CITED

Boisclair, D., and W. C. Leglett. 1989. Among-population variability in fish growth. 1.Influence of the quantity of food consumed. Canadian Journal of Fisheries and Aquatic Sciences 46:457–467.

Brouwer, E., and R. Bobbink. 2002. Restoration of aquatic macrophyte vegetation in acidified and eutrophied softwater lakes: an overview. Aquatic Botany 73:405–431.

Cardinale, B. J., H. Hillebrand, W. S. Harpole, K. Gross, and R. Ptacnik. 2009. Separating the influence of resource "availability" from resource "imbalance" on productivity–diversity relationships. Ecology Letters 12:475–487.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, and P. J. Wright. A. L. Downing, M. Sankaran, and C. Jouseau, editors. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Carignan, R., and R. J. Steedman. 2000. Impacts of major watershed perturbations on aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 57:1–4.

Dixit, A. S., S. S. Dixit, and J. P. Smol. 1996. Setting restoration goals for an acid and metal-contaminated lake: a paleolimnological study of Daisy Lake. Journal of Lake and Reservoir Management 12:323–330.

Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. Ecology Letters 8:301–309.

France, R. L. 1995. Macroinvertebrate standing crop in littoral regions of allochthonous detritus accumulation: implications for forest management. Biological Conservation 71:35–39.

Goulding, M. 1980. The fishes and the forest. University of California Press, Berkeley, California, USA.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Gunn, J. M., P. J. Beckett, W. E. Lautenbach, and S. Monet. 2007. Sudbury, Canada: from pollution record holder to award winning restoration site. Pages 381–408 *in* R. L. France, editor. Handbook of regenerative landscape design. CRC Press, Boca Raton, Florida, USA.

Gunn, J. M., R. Sein, B. Keller, and P. Beckett. 2001. Liming of acid and metal contaminated catchments for the improvement of drainage water quality. Water, Air, and Soil Pollution 130:1439–1444.

Hall, R. O., Jr., J. B. Wallace, and S. L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology 81:3445–3463.

Keller, W., J. H. Heneberry, and S. S. Dixit. 2003. Decreased acid deposition and the chemical recovery of Killarney, Ontario, lakes. Ambio 32:183–189.

Keller, W. B., J. H. Heneberry, and J. M. Gunn. 1999. Effects of emission reductions from the Sudbury smelters on the recovery of acid- and metal-damaged lakes. Journal of Aquatic Ecosystem Stress and Recovery 6:189–198.

Keller, W., N. D. Yan, J. M. Gunn, and J. Heneberry. 2007. Recovery of acidified lakes: lessons from Sudbury, Ontario, Canada. Water, Air, and Soil Pollution Focus 7:317–322.

Luek, A., G. E. Morgan, B. Wissel, J. M. Gunn, and C. W. Ramcharan. 2010. Rapid and unexpected effects of piscivore introduction on trophic position and diet of perch (*Perca flavescens*) in lakes recovering from acidification and metal contamination. Freshwater Biology 55:1616–1627.

Marchant, R. 1989. A subsampler for samples of benthic invertebrates. Bulletin of the Australian Society of Limnology 12:49–52.

Mehner, T., J. Ihlau, H. Dorner, and F. Holker. 2005. Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? Limnology and Oceanography 50:2022–2031.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

Ontario Ministry of the Environment. 1983. Handbook of analytical methods for environmental samples. Volumes 1 and 2. Ministry of Environment Report. Ontario Ministry of the Environment, Toronto, Ontario, Canada.

Pabst, S., N. Scheifhacken, J. Hesselschwerdt, and K. M. Wantzen. 2008. Leaf litter degradation in the wave impact zone of a pre-alpine lake. Hydrobiologia 613:117–131.

Persson, L. 1987. The effects of resource availability and distribution on size class interactions in perch, *Perca fluviatilis*. Oikos 48:148–60.

Prairie, Y. T. 2008. Carbocentric limnology: looking back, looking forward. Canadian Journal of Fisheries and Aquatic Sciences 65:543–548.

Rasmussen, J. B., J. M. Gunn, G. D. Sherwood, A. Iles, A. Gagnon, P. G. C. Campbell, and A. Hontela. 2008. Direct and indirect (foodweb mediated) effects of metal exposure on the growth of yellow perch (*Perca flavescens*): implications for ecological risk assessment. Human and Ecological Risk Assessment 14:317–350.

Rasmussen, J. B., and D. J. Rowan. 1997. Wave velocity thresholds for fine sediment accumulation in lakes, and their effect on zoobenthic biomass and composition. Journal of the North American Benthological Society 16:449–465.

Reynolds, C. 2008. A changing paradigm of pelagic food webs. International Review of Hydrobiology 93:517–531.

Richardson, J. S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. Freshwater Biology 27:169–176.

SARA Group. 2009. Sudbury soils study volume III: ecological risk assessment. ⟨http://www.sudburysoilsstudy.com/EN/indexE.htm⟩

Schindler, D. E., S. R. Carpenter, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, and P. A. Soranno. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. Pages 96–105 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Schindler, D. E., and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. Oikos 98:177–189.

Siefert, J., and M. Mutz. 2001. Processing of leaf litter in acid waters of the post-mining landscape in Lusatia, Germany. Ecological Engineering 17:297–306.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161.

Vanni, M. J., K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. Gonzalez, W. H. Renwick, P. A. Soranno, and R. A. Stein. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. BioScience 55:155–167.

Vanni, M. J., and P. C. de Ruiter. 1996. Detritus and nutrients in food webs. Pages 25–29 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Winterhalder, K., W. E. Lautenbach, and P. Beckett. 2001. The Sudbury regional land reclamation program: a case study. Pages 286–294 *in* J. B. Burley, editor. Environmental design for reclaiming surface mines. Edwin Mellen Press, Queenston, Ontario, Canada.