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Multi-scale analysis of responses of stream macrobenthos to forestry activities and environmental context

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SUMMARY

1. Forestry activities can greatly modify the structure and function of invertebrate communities in streams, but the ability to detect effects of forestry may depend on the spatial scale considered, the choice of response metric and the environmental context. In this study, a multi-scale, multi-metric approach was used to compare the usefulness of proximate and larger-scale measurements of forestry activity for understanding the impacts of forestry on stream macrobenthos.
2. Site-specific responses of macrobenthic communities to forestry activities measured at four spatial scales (sub-basin and 8-, 2- and 0.5-km radii upstream of study sites) were examined for 90 riffle sites distributed among 22 tributary streams (Strahler order 1–5) of the Cascapedia River basin, Quebec, Canada.
3. Multiple regression models and canonical correspondence analysis were used to relate six biological metrics (taxonomic richness, numerical density, biomass density, normalised biomass spectrum, individual body mass and community structure) to variables quantifying logging 1–19 years prior to the study and road density. Environmental predictors (variables quantifying local habitat or landscape features) were included in all analyses to statistically account for environmental context and increase the likelihood of detecting potentially subtle forestry impacts.
4. Forestry activities measured at the larger (sub-basin and 8 km) scales were linked to decline in taxonomic richness, increase in numerical and biomass densities and shift in size structure of benthic macroinvertebrates, indicating that analyses encompassing larger areas, up to the full basin, may allow for more sensitive detection of effects than those of more limited span.
5. These responses primarily reflected marked increases in the abundance of chironomids and decline in the number of trichopteran taxa with increasing areal coverage of recent (≤2–4 years) cuts, suggesting that larger, longer-lived and possibly more specialised taxa were more vulnerable to forestry impacts than smaller, multivoltine, generalist invertebrates. After partialling out the influence of other variables, rapid decline in richness occurred even when <1% of the basin had been clear cut in the year prior to the study.
6. Effects of forestry were detected after statistically accounting for natural environmental variability, which may have otherwise concealed those effects. The combined use of multiple biological metrics, partialling out of environmental effects and measurement of impacts at multiple spatial scales may be a broadly applicable approach for enhancing sensitivity and facilitating interpretation in studies of anthropogenic effects on macroinvertebrate communities.

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Introduction

Forestry activities can greatly modify the structure and function of streams draining affected areas and alter the hydrological balance, geomorphology and streamside vegetation in the basin (Campbell & Doeg, 1989; Vuori & Joensuu, 1996; Buttle & Metcalfe, 2000). Impacts of forestry activities on stream macroinvertebrates are often linked to increases in nutrient concentration, sediment input, water temperature, or light and concomitant changes in the food base (Haefner & Wallace, 1981; Stone & Wallace, 1998; Nislow & Lowe, 2006). Increased sedimentation following forestry activities has been associated with changes in taxonomic richness, density, biomass and species composition of stream macroinvertebrates (Campbell & Doeg, 1989; Haynes, 1999; Death, Baillie & Fransen, 2003). Moreover, changes in macroinvertebrate communities can still be apparent many years after logging has ceased (Silsbee & Larson, 1983). The effects of forestry on stream macroinvertebrates have been examined mostly by comparing logged with reference sites in headwaters or small streams (hydrological order ≤3), usually in areas subjected to clear cutting or intensive logging to the stream edges; comparatively less attention has been paid to streams bordered by buffer strips (Newbold, Ermann & Roby, 1980; Noel, Martin & Federer, 1986; Kreutzweiser, Capell & Good, 2005a). Although cumulative effects of forestry activities in small sub-basins can propagate downstream to the main basin (e.g. increased sedimentation in downstream reaches) (Murphy & Hall, 1981), the effect of forestry activities on macroinvertebrates in larger streams remains poorly investigated.

Because environmental characteristics influence the waterbodies in a basin through mechanistic pathways operating at multiple spatial and temporal scales, understanding of the structure and dynamics of macroinvertebrate communities in streams, including their responses to human disturbance, can be enhanced by examining environmental and anthropogenic effects at multiple scales (Vannote *et al.*, 1980; Allan & Johnson, 1997; Poff, 1997; Malmqvist, 2002; Weigel *et al.*, 2003). Impacts of forestry activities vary according to the environmental characteristics of streams and their surroundings, at various spatial and temporal scales. Clear cutting, including removal of riparian cover, in small, high-gradient, largely shaded streams of the Cascade Mountains in Oregon allowed more light to reach the stream surface, leading to increased primary production and macroinvertebrate abundance. However, the effects of clear cutting on macroinvertebrates were mixed in larger, low-gradient streams of the same region (Murphy & Hall, 1981; Murphy, Hawkins & Anderson, 1981). The larger streams, which have lower gradients and transport capacities, had more sediment accumulation than smaller streams. Removal of the canopy had less effect on instream primary production in the larger streams, probably because their canopy is more open naturally (Murphy & Hall, 1981).

Responses of macroinvertebrate communities to clear cutting can also depend on local habitat features such as substratum size. In a second-order Appalachian stream, the number of taxa showing increased density following logging was greatest on large, more physically stable substrata, whereas the number of taxa showing decline in density was greatest on smaller, less stable substrata (Gurtz & Wallace, 1984). Furthermore, the rate of recovery from clear cutting of macroinvertebrate communities may differ among habitat types. Macroinvertebrate communities in riffle and depositional habitats of mountain streams in North Carolina took much longer to recover from logging disturbance than those on moss-covered bedrock, a more stable habitat (Stone & Wallace, 1998). Clearly, environmental context should be considered when evaluating forestry impacts, which may otherwise be masked by natural variation among sites. In observational studies that examine variation across multiple sites in a survey, statistical tools for isolating the effect of a variable by holding constant or controlling, by statistical means, the effects of all other variables included in the analysis (i.e. 'partialling out' those effects), can facilitate detection of the effects of interest (Rodríguez & Magnan, 1995).

The ability to detect effects of forestry may also depend on the choice of response metric, because different characterisations of benthic communities, such as the biomass spectrum and taxonomic community structure, can emphasise different aspects of ecological processes (e.g. whether structure is influenced by habitat or size-dependent mechanisms: Rodríguez & Magnan, 1993). Therefore, evaluation of a wide range of biological metrics is useful in detecting and understanding the impact of forestry, as well as the response and subsequent recovery of macroinvertebrate communities (Resh *et al.*, 1988; Stone & Wallace, 1998; Kreutzweiser, Capell & Good, 2005b).

In this study, a multi-scale, multi-metric approach was used to compare the usefulness of proximate and larger-scale measurements of forestry activity for understanding the impacts of forestry on stream macrobenthic communities at the site scale. Specifically, because effects of forestry activities in a stream basin can be cumulative and propagate over long distances, measurements of forestry variables integrated over larger areas upstream from the study sites were expected to be better predictors of impact than local measurements. Multiple regression and canonical correspondence analysis were use to examine site-specific responses of macrobenthic communities to forestry activities occurring 1–19 years prior to the study, measured at four spatial scales (sub-basin, and 8-, 2- and 0.5-km radii upstream of study sites). Six different biological metrics, taxonomic richness, numerical density, biomass density, slope of the normalised biomass spectrum (a summary measure reflecting the balance of processes such as reproduction, growth and mortality; Kerr & Dickie, 2001), individual body mass and taxonomic community structure, were used to assess the responses. Environmental predictors were included in all quantitative analyses to statistically account for environmental context and increase the likelihood of detecting potentially subtle forestry impacts.

Methods

The Cascapedia River basin, Quebec, Canada, drains an area of 3172 km^2. Plant cover in the basin consists primarily of forest (conifer: 69%; mixed: 17%; scattered deciduous: 1%), with the remaining area accounted for by shrubs, rocks and other non-forest cover (13%). The basin is sparsely populated but is subject to intensive forestry activities. Of the 90 sites in the present study, 87 were in sub-basins exposed to logging in the 19 years preceding the study. Substantial portions of the sub-basins upstream from the study sites (sub-basin area: median = 74.8 km^2; range = 8.1–337.9 km^2) were affected by clear cutting (percentage cover of cuts: median = 22.7%; range = 0.0–43.1%) or partial cutting (median = 8.4%; range = 0.0–23.0%) over this period. Governmental regulations have required forestry operations in the basin to leave unharvested a 20-m buffer strip (60-m when Atlantic salmon is present) along permanent streams since 1988.

In all, 90 riffle sites (45 in 2001; 45 in 2002), distributed among 22 tributary streams (Strahler order range = 1–5; stream order ≥3 at 90% of the study sites), were sampled at low flow in two consecutive years (17 July–2 September 2001; 16 July–1 August 2002). At each site, two points were selected randomly along each of three transects drawn transversely to the stream at 5-m intervals. Macroinvertebrates were sampled at each point (12-B92 Surber sampler, 500 μm mesh, 0.0929 m^2 sampling area; Wildlife Supply Company, Buffalo, NY, U.S.A.) during the daytime (9:00–17:00 hours), by hand-scrubbing the rocks contained within the frame of the sampler. Surber samples from the six points at each site were pooled prior to the calculation of biological metrics. All collected organisms were preserved in 3.7% formaldehyde and identified in the laboratory, to genus when feasible, following Wiggins (1977), Peckarsky *et al.* (1990), Merritt & Cummins (1996) and Thorp & Covich (2001). Total length of individual organisms from the extremity of the head to the end of the abdomen, excluding cerci and antenna, was measured to the nearest 0.01 mm. Dry mass (DM) (mg) of individuals was calculated using published mass-length relations (Smock, 1980; Tower, Henderson & Veltman, 1994; Hodar, 1996; Benke *et al.*, 1999; Johnston & Cunjak, 1999; Stead, Schmid-Araya & Hildrew, 2003). For pupal stages, mass-length relations were developed following Benke *et al.* (1999). Incomplete individuals were assigned the mean DM of complete individuals in their taxon.

A set of 18 descriptors of local habitat or landscape features was quantified at each site (Table 1). Water depth was measured at the middle transect at five equidistant points. Current velocity (FP 101 flow probe, Global Water, Gold River, CA, U.S.A.) was measured at three equidistant points on the three transects. Wetted width was measured at each transect. Water temperature was measured at the centre of the middle transect (hand-held thermometer). Mean substratum size (modified Wentworth scale) was

Table 1 Summary statistics for biological metrics (dependent variables) and habitat or landscape descriptors (independent variables) in multiple regression analyses. $n = 90$ riffle sites in tributary streams of the Cascapedia River.

Variable type Variable name	Median	25%, 75% quartiles	Min., Max.
Biological metric			
Rarefied taxonomic richness	13.8	(12.3, 15.6)	(7.2, 27.7)
Numerical density (number m^{-2})	2068.5	(1273.8, 3189.8)	(134.6, 28891.6)
Biomass density (mg DM m^{-2})	719.4	(397.5, 2163.5)	(68.7, 5430.3)
Slope of normalised size spectrum	−0.83	(−0.89, −0.75)	(−1.21, −0.48)
Median individual mass (mg DM)	0.165	(0.054, 0.384)	(0.018, 0.732)
Habitat or landscape descriptor			
Altitude (m)	265	(200, 320)	(0, 410)
Canopy opening (°)	96.8	(78.2, 114.2)	(52.1, 141.5)
Distance to mainstem (km)	13.5	(4.2, 23.8)	(0.1, 48.5)
Distance to source (km)	16.8	(8.8, 26.3)	(1.9, 59.6)
Entrenchment (%)	10	(5, 20)	(0, 55)
Height increment at flood (m)	0.5	(0.4, 0.6)	(0.2, 1.4)
Mean current velocity (cm s^{-1})	51	(34, 76)	(8, 138)
Mean depth (cm)	28	(21, 34)	(9, 51)
Mean substratum size (index*)	5.3	(4.7, 5.6)	(3.0, 6.6)
Mean water temperature (°C)	9.8	(8.0, 11.2)	(7.0, 13.8)
Mean wetted width (m)	9.3	(5.1, 15.7)	(1.8, 32.0)
Stream order	3	(3, 4)	(1, 5)
Stream slope (°)	0.8	(0.5, 1.0)	(0.0, 4.0)
Units of large woody debris (number)	6.8	(1.0, 8.0)	(0.0, 45.0)
Valley width (m)	180	(100, 360)	(20, 1820)
Vegetation abundance in sample (index)	1.5	(1.0, 3.0)	(1.0, 5.0)
Vegetation abundance in site (index)	1.0	(1.0, 1.8)	(1.0, 4.0)
Width increment at flood (m)	2.7	(2.0, 4.0)	(0.4, 22.4)

*Modified Wentworth scale.

assessed visually at each site. Abundance of submerged vegetation (moss or macrophytes) at each site was estimated visually and assigned ordinal values reflecting areal coverage (1, ≤5%; 2, 6–15%; 3, 16–45%; 4, >45%). Abundance of vegetation within the frame of the Surber sampler was similarly assigned ordinal codes (1, absence; 2, 1–25%; 3, 26–50%; 4, 51–75%; 5, >75% of sub samples). Canopy opening (angle between riparian tree tops at the centre of the stream) and slope over the stream reach were measured with a hand-held clinometer (PM-5; Suunto, Vantaa, Finland). The height and width increments at flood (from annual flood marks) were measured on site. Entrenchment (mean gradient ≤100 m away from stream bank), stream order (Strahler scale), valley width (lateral extent of terrace) and altitude were obtained from 1 : 20 000 topographic maps (Quebec Topographic Database), as were distances by waterway from each site to the Cascapedia River ('distance to mainstem') and to the stream source ('distance to source') (6125 planimeter; Calculated Industries Inc., Carson City, NV, U.S.A.). Units of large woody debris (>10 cm diameter) were counted at each site.

A geographic information system (ArcGIS, v. 8.2, ESRI, Redlands, CA, U.S.A.) was used to measure landscape features and forestry activities at four spatial scales: sub-basin, and semi-circular zones of 8-, 2- and 0.5-km radii upstream of each site (Fig. 1). The landscape variables were stream gradient (mean slope from site to limit of the upstream zone), area of the upstream zones (ha) and per cent areal coverage of conifers and of deciduous vegetation. Logging activities were grouped into two categories reflecting the harvesting procedures employed by forestry companies: clear cuts (clear cut harvesting, protection of regeneration, seed tree and patch cutting) and partial cuts (partial harvesting, thinning, strip harvesting, selection cutting, harvesting within green strips and diameter-limit cutting). The forestry variables used in the analyses quantified logging (per cent areal coverage of clear cuts and partial cuts in the following time intervals preceding the study: 1, 2–4, 5–9, 10–14 and 15–19 years) and the density of roads (km km^{-2}) and of road crossings with streams (crossings km^{-2}).

Separate multiple regressions were used to relate five biological metrics, rarefied taxonomic richness,

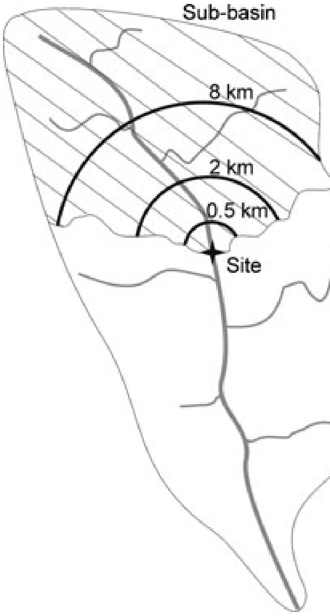

Fig. 1 Schematic representation of zones used to quantify landscape features and forestry activities at four spatial scales: sub-basin and 8-, 2- and 0.5-km radii upstream of the sampling sites. The concentric curves are delimited by watershed boundary lines.

numerical and biomass densities, slope of the normalised biomass spectra and median individual mass, to environmental and forestry variables (Table 1). Sampling year was included as an additional independent variable to account for possible interannual differences. Regression models were built for each metric at each of the four spatial scales, for a total of 20 models. Prior to quantitative analyses, all variables were examined graphically and transformed when necessary to meet statistical assumptions. A stepwise procedure (forward selection; cut off for variable entry or removal at nominal $P \leq 0.05$) was used to determine which predictors to retain in the final regression models (program SYSTAT, v. 10.2; SPSS Inc., 2002). The tolerance for predictors in final models always exceeded 0.65, indicating only mild collinearity among predictors (Tabachnick & Fidell, 2000). Conditional relationships between the response variable and individual predictors were examined by fixing all other predictors at their mean value to partial out their influence.

To account for differences in abundance among sites (range: 74–4978 individuals), taxonomic richness was obtained by rarefaction to a sample of 74 individuals (mean of 1000 trials, program ECOSIM v. 7; Gotelli & Entsminger, 2004). To characterise biomass spectra, 13 biomass classes were established to cover the entire range of individual mass in the samples (<0.08–441.66 mg DM). Class boundaries were on a $\log_2$ scale, with class 1 corresponding to body mass ≤0.08 mg DM and class 13 corresponding to body mass ≥327.44 mg DM. Biomass spectra were generated by summing, for each biomass class, the mass of all organisms falling within the class, regardless of taxonomic affiliation. Normalised biomass spectra were generated by calculating for each biomass class the expression $\log_2$(total biomass in class/class range). Least-squares linear regressions of this expression on $\log_2$(upper limit of biomass class) were calculated and the regression slopes used to quantify differences in spectra among sites (Hanson, 1990; Rodríguez & Magnan, 1993; Zimmer *et al.*, 2001).

Separate canonical correspondence analyses (CCA) were performed to relate taxonomic community structure (relative abundances, based on numerical density) to environmental and forestry variables at the four spatial scales (program CANOCO, v. 4.5; ter Braak & Smilauer, 2002). Sampling year was included as a covariable in all final models to statistically account for interannual differences (Magnan *et al.*, 1994). The forward selection procedure implemented in CANOCO (cut off at nominal $P = 0.05$) was used to determine which predictors to retain. The variance inflation factor for predictors in final models was always <5, indicating only mild collinearity among predictors (ter Braak & Smilauer, 2002). Significance values for individual variables and for the sum of all eigenvalues were determined by Monte Carlo tests (2000 permutations). In all quantitative analyses, sampling date, the number of days elapsed since 1 July, was included as a predictor to account for potential seasonal trends.

Results

Rarefied taxonomic richness was negatively associated with canopy opening and stream gradient at the 0.5-km scale, but no environmental influences on richness were detected at other scales (Table 2). Among the forestry variables, only 1 year clear cuts was retained in the final models at all scales and was negatively associated with richness. Irrespective of scale, richness increased along a gradient from recent (1 year) to older (≥10 year) cuts, as indicated by the opposite signs of standardised coefficients for recent

Table 2 Standardised coefficients and associated *P* values (in parentheses) of environmental and forestry predictors in regression models for the rarefied taxonomic richness, numerical density, biomass density, slope of normalised biomass spectra and median individual mass of benthic macroinvertebrates, at four spatial scales: sub-basin, 8-, 2- and 0.5 km. R^2 is given for each model. All model *P* values are <0.001.

Biological metric	Spatial scale (radii upstream of site)			
Variable name	Sub-basin	8 km	2 km	0.5 km
Rarefied taxonomic richness				
Canopy opening				−0.179 (0.046)
Sampling date	−0.233 (0.015)	−0.284 (0.002)	−0.297 (<0.001)	−0.359 (<0.001)
Stream gradient				−0.257 (0.004)
% 1-year clear cuts	−0.384 (<0.001)	−0.266 (0.002)	−0.171 (0.040)	−0.184 (0.030)
% 2- to 4-year partial cuts	−0.305 (0.003)			
% 10- to 14-year partial cuts	0.318 (0.002)	0.390 (<0.001)		
% 15- to 19-year clear cuts			0.491 (<0.001)	0.407 (<0.001)
% 15- to 19-year partial cuts	0.204 (0.030)			
R^2	0.386	0.413	0.447	0.479
Numerical density				
Distance to mainstem		0.301 (0.006)	0.378 (0.001)	0.378 (0.001)
Valley width	0.184 (0.035)			
Vegetation in sample	0.310 (<0.001)	0.290 (0.004)	0.300 (0.004)	0.300 (0.004)
Vegetation in site		0.308 (0.002)	0.326 (0.002)	0.326 (0.002)
Water temperature	−0.213 (0.015)	−0.393 (<0.001)	−0.399 (<0.001)	−0.399 (<0.001)
Width at flood			−0.189 (0.044)	−0.189 (0.044)
% 2- to 4-year partial cuts	0.395 (<0.001)	0.262 (0.004)		
% 15- to 19-year partial cuts	0.213 (0.015)			
R^2	0.449	0.437	0.406	0.406
Biomass density				
Altitude	0.176 (0.029)	0.172 (0.020)		
Distance to mainstem			0.320 (<0.001)	0.259 (0.006)
Mean wetted width	0.398 (<0.001)		0.530 (<0.001)	0.526 (<0.001)
Stream gradient		−0.361 (<0.001)		
Vegetation in site	0.210 (0.008)			0.185 (0.045)
Water temperature		0.282 (<0.001)		
% 1-year clear cuts			0.164 (<0.001)	
% 5- to 9-year partial cuts	0.379 (<0.001)	0.366 (<0.001)	0.224 (0.005)	0.189 (0.025)
R^2	0.566	0.595	0.547	0.479
Slope of normalised biomass spectrum				
Vegetation in sample	−0.380 (<0.001)	−0.342 (<0.001)	−0.494 (<0.001)	−0.494 (<0.001)
Water temperature	0.302 (0.001)	0.277 (0.002)	0.261 (0.009)	0.261 (0.009)
Width at flood			0.200 (0.039)	0.200 (0.039)
% 2- to 4-year clear cuts	−0.192 (0.037)	−0.258 (0.005)		
% 2- to 4-year partial cuts	−0.391 (<0.001)	−0.328 (<0.001)		
% 15- to 19-year partial cuts		−0.227 (0.011)		
R^2	0.423	0.423	0.329	0.329
Median individual mass				
Altitude	0.218 (0.007)		0.218 (0.007)	
Mean velocity		0.215 (0.012)		
Vegetation in site	−0.237 (0.003)		−0.237 (0.003)	−0.202 (0.010)
Water temperature	0.693 (<0.001)	0.530 (<0.001)	0.693 (<0.001)	0.706 (<0.001)
% conifers				0.212 (0.006)
% 1-year partial cuts		−0.218 (0.005)		
R^2	0.556	0.568	0.556	0.556

and older cuts. After partialling out statistically the influence of other variables, richness showed a non-linear decline with increases in 1 year clear cuts, with the most rapid change occurring at the lowest values (<1%) of clear cuts (Fig. 2). At all scales, richness declined over the summer. The amount of variation

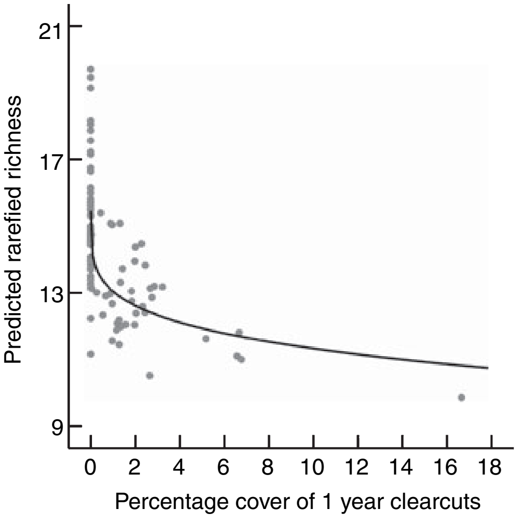

Fig. 2 Conditional relationship between the rarefied taxonomic richness and the proportion of 1-year clear cuts at the sub-basin scale. Predicted values (line) were obtained from the multiple regression model for rarefied taxonomic richness by fixing all independent variables other than 1-year clear cuts at their means. Partial residuals (grey symbols) are shown also.

accounted for by the models (R^2) declined progressively from smaller to larger scales (Table 2).

Numerical density was negatively related to water temperature and positively related to vegetation in the sample, at all spatial scales (Table 2). Numerical density also was positively related to distance to mainstem and vegetation in site and negatively related to width at flood, which had detectable influence at the smaller spatial scales but not at the sub-basin scale. Numerical density was positively related to two forestry variables (2- to 4-year and 15- to 19-year partial cuts) but only at the larger spatial scales.

Biomass density was positively associated with mean wetted width at the largest scale and the two smallest spatial scales; generally, the associations between biomass density and the environmental variables retained in the final models did not appear to vary systematically across scales (Table 2). Biomass density showed positive relationships with 5- to 9-year partial cuts at all scales, and with 1-year clear cuts at the 2-km scale.

The slope of the normalised biomass spectrum was positively related to temperature and negatively related to vegetation in the sample at all scales, a pattern opposite to that for numerical density (Table 2). The slope of the spectrum was positively related to width at flood only at the two smaller scales. The slope of the spectrum was negatively related to recent (2–4 year) or older (15–19 year) cuts at the two larger spatial scales. Because the slope and the intercept of the biomass spectra were negatively correlated (Pearson $r = -0.66$, $n = 90$), steeper slopes indicate increase in the numerical abundance of smaller organisms rather than decline in that of larger organisms. Therefore, variables with positive regression coefficients are positively related to body size. Increased logging was thus associated with a shift in size structure favouring smaller organisms at the two larger spatial scales.

Median individual mass, a measure of body size, was positively related to temperature at all scales and was positively related to altitude and mean water velocity and negatively to vegetation in site at various scales; none of these relations appeared to depend systematically on scale (Table 2). Inferences on the influence of water temperature, vegetation and recent cuts on median individual mass were therefore similar to those obtained previously from the analysis of biomass spectra. Median individual mass was positively associated with conifer cover at the 0.5-km scale. Among the forestry variables, only 1 year partial cuts (negative relation at the 8-km scale) seemed to influence median individual mass.

Considered jointly, the multiple regression analyses indicate that logging led to decline in taxonomic richness, increase in numerical and biomass densities and shift in size structure of benthic macroinvertebrates at the sub-basin and 8-km scales. These changes were accounted for mostly by marked increases in the abundance of chironomids in response to logging. Chironomids, the majority of which (66.7%) were in the Orthocladiinae, accounted for 44.5% of total numerical abundance summed across sites. Chironomids predominated numerically in the smaller biomass size classes and their median individual mass (0.059 mg DM) was considerably less than that of non-chironomid taxa (0.392 mg DM) (Fig. 3a). Separate multiple regression models relating the numerical proportion and the numerical density of chironomids to environmental and forestry variables at the sub-basin scale showed that both the proportion and the numerical density were positively associated with 1-year clear cuts and 2- to 4-year partial cuts (Table 3). The models indicated that after partialling out the environmental effects, the most rapid change in

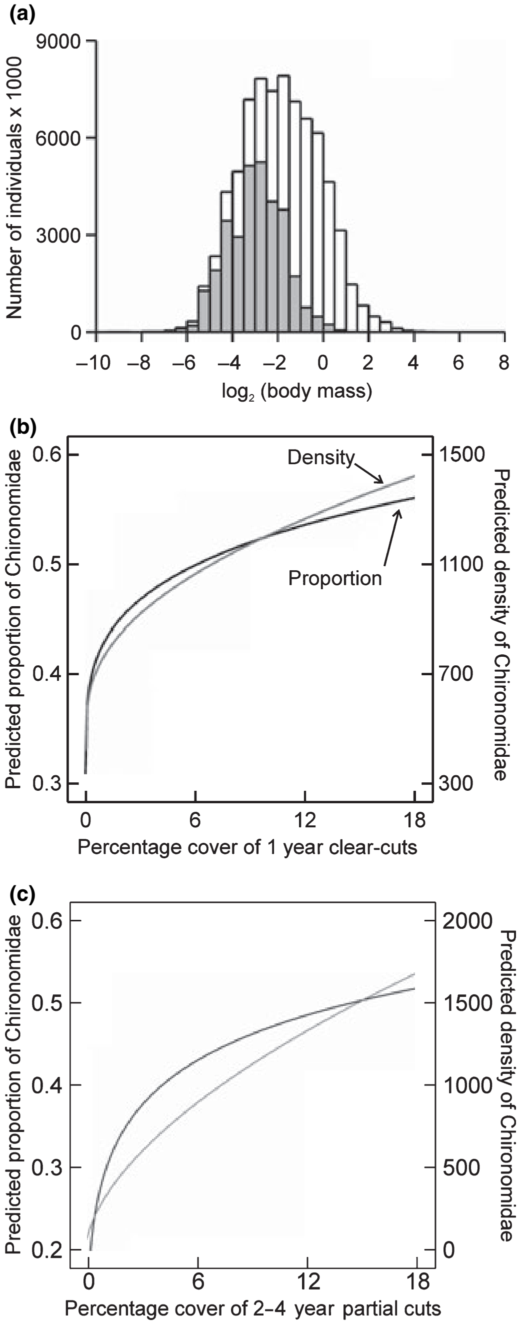

Fig. 3 (a) Frequency distribution of individual mass (mg DM m^{-2}) for Chironomidae (grey bars) and all taxa combined (open bars). (b) Conditional relationship between the numerical proportion (black line) and numerical density (number m^{-2}; grey line) of Chironomidae and the proportion of 1-year clear cuts, at the sub-basin scale. (c) Conditional relationship between the numerical proportion (black line) and numerical density (number m^{-2}; grey line) of Chironomidae and the proportion of 2- to 4-year clear cuts, at the sub-basin scale. In (b) and (c), predicted values were obtained from the multiple regression models for proportion and density by fixing all independent variables other than 1 year or 2- to 4-year clear cuts at their means.

Table 3 Standardised coefficients and associated *P* values of environmental and forestry predictors in multiple regression models for the numerical proportion and numerical density of Chironomidae, at the sub-basin scale. The proportion was transformed as arcsin $(P)^{0.5}$ and the density as $\ln(X + 1)$. R^2 is given for each model. The model *P* value is <0.001 for both models.

Variable name	Standardised coefficient (*P*)
Numerical proportion	
Mean depth	−0.256 (0.007)
Vegetation in sample	0.303 (<0.001)
Vegetation in site	0.215 (0.014)
Water temperature	−0.445 (<0.001)
% 1-year clear cuts	0.301 (<0.001)
% 2- to 4-year partial cuts	0.293 (0.001)
R^2	0.584
Numerical density	
Vegetation in sample	0.335 (<0.001)
Vegetation in site	0.281 (0.002)
Water temperature	−0.501 (<0.001)
Woody debris	−0.175 (0.043)
% 1-year clear cuts	0.245 (0.002)
% 2- to 4-year partial cuts	0.364 (<0.001)
R^2	0.596

both proportion and density occurred at very low (<1%) values of percentage cover for both 1-year clear cuts (Fig. 3b) and 2- to 4-year partial cuts (Fig. 3c).

Final CCA models were broadly similar at all spatial scales; therefore, results are presented only for the sub-basin scale (Fig. 4a–d, Table 4). Among the environmental variables, vegetation in the sample and in the site, substratum size, distance to source and woody debris had the strongest correlations with the first two ordination axes, as indicated by the length of the corresponding arrows in the ordination plot (Fig. 4a,b). Two forestry variables, 1-year clear cuts and 15- to 19-year clear cuts, had high correlations with the first ordination axis and appeared to define a gradient contrasting old and recent cuts (Fig. 4a). The only clear pattern in the distribution of major taxonomic groups on the ordination figure was for trichopteran taxa, which showed a shift away from sites with high proportion of 1-year clear cuts (Fig. 4c). The ordination plot indicates that only 7 of 37 trichopteran taxa had peak modal abundance in sites with a high proportion of 1-year clear cuts, contrasting with a more even distribution, 46 of 101, for non-trichopteran taxa (Fisher's exact test, $P = 0.005$). A separate multiple regression of the number

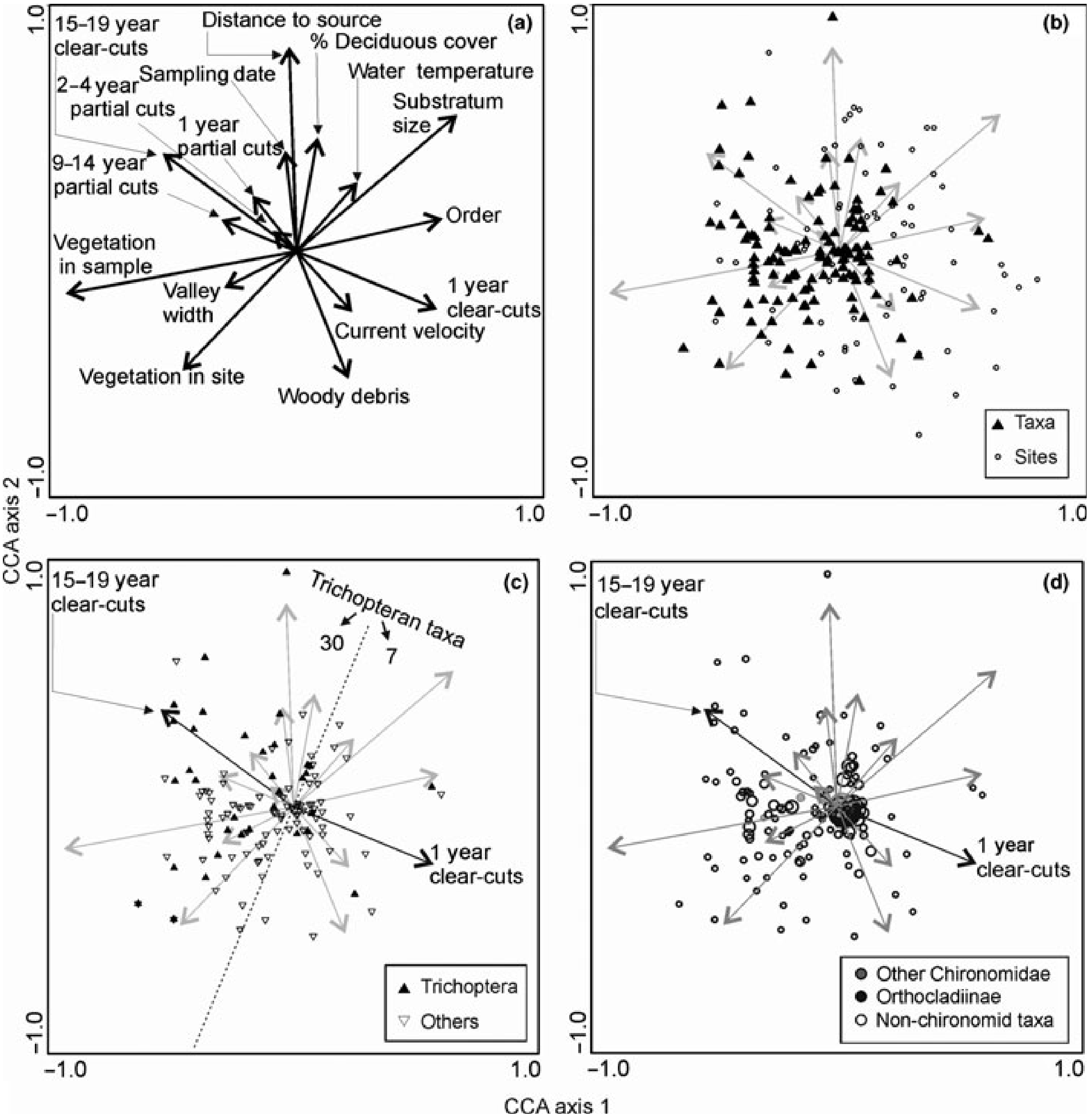

Fig. 4 Canonical correspondence analysis ordination of sites, macroinvertebrate taxa and environmental and forestry variables at the sub-basin scale. (a) Arrow plot of environmental variables showing correlations of variables with the axes (length of the projection of the arrow onto axis) and correlations between variables (angles between arrows). The origin coincides with mean values of the transformed variables. (b) Triplot showing the distribution of taxa and sites in relation to environmental and forestry variables. (c) Biplot showing the distribution of Trichoptera and other taxa in relation to forestry variables: 30 of 37 trichopteran taxa are to the left of the dashed line orthogonal to the arrow for 1-year clear cuts, indicating negative association with 1-year clear cuts. (d) Bubble plot showing the relative abundance (proportional to circle size) of Orthocladiinae (black symbols), other Chironomidae (grey symbols) and non-chironomid taxa (empty symbols).

of trichopteran taxa on the proportions of 1 year and 15- to 19-year clear cuts for the 90 riffle sites also pointed to an association of trichopteran richness with 1 year clear cuts (partial standardised coefficient, $b_{1\ \text{year}} = -0.21$, $P = 0.02$) and 15- to 19-year clear cuts ($b_{15\text{–}19\ \text{year}} = 0.48$, $P < 0.001$). The positive relationship previously detected in the multiple regression analyses between chironomid abundance and 1-year clear cuts was not readily apparent from the distribution of peak modal abundances of chironomid taxa, which were concentrated near the origin in the CCA ordination (Fig. 4d).

Table 4 Summary results of canonical correspondence analysis for macroinvertebrate taxa (based on numerical density) at the sub-basin scale, for 90 riffle sites sampled in 2001 and 2002. Sampling year was included as a covariate in the analysis.

	Axis 1	Axis 2	Total variation
Eigenvalue	0.163	0.108	2.708
Taxon-environment correlation	0.802	0.913	
Cumulative percent variation of taxon data	6.4	10.6	
Cumulative percent variation of taxon-environment relation	21.4	35.6	
P-value of the Monte Carlo permutation test of significance	0.0005	0.0005	
Sum of all eigenvalues after extraction of covariable effect			2.543
Sum of all canonical eigenvalues			0.762

Discussion

The main finding of this study is that logging activities measured at the sub-basin and 8-km scales were linked to decline in taxonomic richness, increase in numerical and biomass densities and shift in size structure of benthic macroinvertebrates. These changes primarily reflected marked increases in the abundance of chironomids and decline in the number of trichopteran taxa, with increasing areal coverage of recent cuts.

The results suggest that larger, longer-lived and possibly more specialised taxa, in particular trichopterans, were more vulnerable to forestry impacts and were replaced at recently logged sites by smaller, multivoltine, less specialised invertebrates, such as the Orthocladiinae and other chironomids. The taxonomic diversity of macroinvertebrates generally declines following a natural or anthropogenic disturbance and increases with later recovery (Stone & Wallace, 1998). Modification of a river basin as a consequence of forestry activities may favour organisms with broad tolerance over more specialised organisms, or, transiently, faster colonisers, allowing a few successful species to become dominant and leading to decline in diversity (Hawkins, Murphy & Anderson, 1982; Gurtz & Wallace, 1984; Gregory *et al.*, 1987). A comparison of the effects of flooding in desert streams (Fisher *et al.*, 1982), a natural disturbance, and clear cuts in southern Appalachian streams, an anthropogenic disturbance, found similar early successional characteristics of invertebrate communities, such as dominance by small, short-lived, generalist invertebrates, under both types of disturbance (Gurtz & Wallace, 1984). The effects of clear cuts included rapid increase in multivoltine generalist feeders such as chironomids and decline in taxa having lower fecundity, more specialised feeding and slower development (Gurtz & Wallace, 1984). Similarly, an increase in fine sediment inputs from a logging road led to reduction in taxonomic richness resulting from a decline in the proportion of shredders and an increase in that of chironomids (Kreutzweiser *et al.*, 2005b). Shifts in the size structure and taxonomic composition of invertebrate prey resulting from logging activities may affect secondary consumers such as fish by modifying the availability of energetically profitable items in the benthos or the drift (Poff & Huryn, 1998).

Effects of forestry activities on macroinvertebrate communities were detected up to 15–19 years after logging. Stream recovery is closely linked to the long-term processes of forest regrowth and formation of debris dams in small streams (Yount & Niemi, 1990; Stone & Wallace, 1998) and may lag behind recovery of the impacted terrestrial part of the basin (Gurtz & Wallace, 1984). Differences in macroinvertebrate communities between logged and unlogged stream basins may persist for decades after logging has ceased (Haefner & Wallace, 1981; Silsbee & Larson, 1983). In the present study, taxonomic richness declined with recent (≤4 years) cuts but increased with older (10–19 years) cuts, suggesting that after initial depression during the first years after logging, macroinvertebrate diversity may be enhanced in areas undergoing regrowth.

Responses of univariate biological metrics varied among spatial scales. Specifically, effects of forestry activities on three of the metrics, numerical density, slope of biomass spectrum and median individual mass, were only apparent at the sub-basin or 8-km scales. Impacts of forestry activities, such as increases in sediment and nutrient inputs, can be propagated over long distances and influenced by riparian or basin-wide conditions along the whole length of a stream and its tributaries (Allan, 2004). For example, increases in sediment load generated by logging activities in headwater areas can be exported cumulatively downstream to low-gradient, larger reaches, where they may affect macroinvertebrate communities (Murphy & Hall, 1981; Buttle & Metcalfe, 2000). When effects of logging are cumulative, or are manifest mostly at sites distant from the logged area, measures that quantify logging activities over a large spatial scale, up to the full basin area, may therefore allow for more sensitive detection of logging effects on macroinvertebrates than measures spanning a more restricted scale. As a corollary, focusing research efforts on detecting forestry effects solely at a local scale may prove unproductive in large basins.

Most studies of the effect of logging on stream macroinvertebrates have focused on small, first or second order headwater streams (Graynoth, 1979; Newbold *et al*., 1980; Haefner & Wallace, 1981; Gurtz & Wallace, 1984; Noel *et al*., 1986; Stone & Wallace, 1998; Death, Baillie & Fransen, 2003; Kiffney, Richardson & Bull, 2003; Nislow & Lowe, 2006), in contrast with the present study in which most streams were of third order or larger. The observed responses of macroinvertebrate communities to logging were therefore likely unrelated to increased primary production in response to increased light penetration (Stone & Wallace, 1998; Nislow & Lowe, 2006), because in larger streams the canopy is naturally open and light penetration has less influence on primary production (Vannote *et al*., 1980; Murphy & Hall, 1981). Furthermore, all streams were bordered by 20- or 60-m buffer strips and no effects of canopy opening were detected in the statistical analyses. In agreement with previous work showing abiotic and biotic responses to logging in streams protected by 30-m buffer strips (Kiffney *et al*., 2003), the presence of buffer strips in the present study seemed insufficient to completely eliminate impacts of logging activities on macroinvertebrate communities.

In field studies relying on observational data, naturally variable environmental influences can be held constant statistically to facilitate detection of forestry impacts. Effects of forestry activities on macroinvertebrates in this study were detected after accounting for environmental variability that may have otherwise concealed those effects. The examination of predicted forestry effects with environmental influences partialled out proved fruitful in the present study, for example, by showing that taxonomic richness may decline very rapidly in response to logging even if only small portions of basins are affected (Kiffney *et al*., 2003). The combined use of multiple biological metrics and partialling out of environmental effects to examine forestry effects on macroinvertebrate communities at multiple spatial scales can be a useful approach for enhancing sensitivity and facilitating interpretation of results in future studies as well.

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