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RÉPONSES DES COMMUNAUTÉS DE MACROINVERTÉBRÉS DES RUISSEAUX AUX ACTIVITÉS FORESTIÈRES ET AU CONTEXTE ENVIRONNEMENTAL À DIFFÉRENTES ÉCHELLES SPATIALES

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RÉSUMÉ

Nous avons examiné, à l'aide des régressions multiples et d'analyses canoniques des correspondances, l'influence des activités forestières et des variables environnementales sur la richesse taxonomique, la densité, la biomasse, le spectre de biomasse, la biomasse médiane et la structure des communautés de macroinvertébrés de la rivière Grande Cascapédia. En 2001 et 2002, nous avons récolté des invertébrés dans 90 sites répartis sur 22 ruisseaux tributaires. Nous y avons également mesuré un ensemble de variables environnementales et quantifié, par système d'information géographique, des interventions forestières, dans des rayons d'influence de 0,5 km, 2 km, 8 km et pour l'ensemble bu bassin versant en amont des sites. L'importance relative et l'effet des activités forestières variaient fortement en fonction de la variable biologique étudiée et de l'échelle spatiale. L'impact des coupes récentes sur la structure des communautés était généralement plus important aux plus grandes échelles. Malgré la présence de bandes riveraines, lorsque la proportion de coupes récentes ($\leq$ 4 ans) augmentait, il y avait une diminution de la richesse et de la taille des macroinvertébrés, alors que la densité et la biomasse augmentaient, tout comme la proportion et la densité de chironomidés. La majorité des taxons de trichoptères étaient également reliés négativement aux coupes d'un an. Cependant, la richesse taxonomique était reliée positivement aux coupes plus anciennes (10-20 ans), ce qui suggère la rémission des communautés de macroinvertébrés après la régénération du milieu terrestre. Ces résultats indiquent que la capacité à déceler les impacts des activités forestières sur le milieu aquatique dépend du contexte environnemental et qu'elle peut varier en fonction de la variable biologique et de l'échelle spatiale de l'étude.

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AVANT-PROPOS

Ce mémoire comprend deux chapitres. Le premier chapitre est une synthèse en français du projet de maîtrise. Le second chapitre est un article qui sera soumis pour publication dans le périodique Freshwater Biology, et qui présente les résultats essentiels de mon projet de maîtrise.

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INTRODUCTION

Les caractéristiques du paysage influencent les cours d'eau d'un bassin selon différents mécanismes opérant à plusieurs échelles spatiales et temporelles (Vannote *et al.*, 1980; Allan & Johnson, 1997; Weigel *et al.*, 2003). Ainsi, des facteurs à l'échelle régionale, comme la géologie du bassin versant, vont contraindre d'autres facteurs à l'échelle locale, comme la composition du substrat du lit d'une rivière (Weigel *et al.*, 2003). Comme la structure des communautés d'invertébrés reflète les caractéristiques de leur environnement, elle est également influencée par des facteurs agissant à plusieurs échelles spatiales (Malmqvist, 2002). Ainsi, les espèces trouvées dans un habitat donné sont en quelque sorte filtrées par ces facteurs et représentent un sous-échantillon de l'ensemble des espèces d'une région (Malmqvist, 2002). Pour comprendre et mieux prédire les réponses des communautés de macroinvertébrés aux perturbations d'origine anthropique, il est important d'examiner comment les facteurs opérant à différentes échelles influencent les communautés de macroinvertébrés (Poff, 1997; Weigel *et al.*, 2003).

Les activités forestières peuvent altérer les ruisseaux (Resh *et al.*, 1988; Campbell & Doeg, 1989), même si ces derniers ne sont pas directement touchés (Vuori & Joensu, 1996). Les activités forestières peuvent modifier le débit, la géomorphologie et la composition du substrat des ruisseaux, ainsi que contribuer à une augmentation de la concentration en nutriments, de la sédimentation, de l'accumulation de débris, des particules en suspension, des ions dissous et de la température des ruisseaux (Vuori & Joensuu, 1996; Buttle & Metcalfe, 2000). À leur tour, ces changements peuvent affecter les communautés de macroinvertébrés.

Les impacts des activités forestières peuvent varier avec les caractéristiques des ruisseaux et du milieu terrestre. Dans de petits ruisseaux ombragés et à forte pente, les coupes à blanc impliquant l'enlèvement de la bande riveraine ont amené une augmentation de la production primaire qui a à son tour conduit à une hausse de l'abondance des macroinvertébrés (Murphy & Hall, 1981; Murphy, Hawkins & Anderson, 1981). Dans de plus grands ruisseaux à faible pente, l'enlèvement de la bande riveraine par les coupes à blanc n'a amené qu'une faible augmentation de la production primaire et les effets des coupes sur les macroinvertébrés étaient plutôt reliés à l'accumulation des sédiments (Murphy & Hall, 1981). Pour ces raisons, il s'avère important de tenir compte des différences dans les caractéristiques environnementales entre les sites pour faciliter la détection des impacts des coupes. Autrement, les effets des activités forestières pourraient être masqués par la variabilité environnementale (Rodriguez & Magnan, 1995).

Il est connu que différents descripteurs des communautés de macroinvertébrés, tels la structure taxonomique et les spectres de taille, peuvent mettre en évidence des processus écologiques très différents (Rodríguez & Magnan, 1993). Afin de déceler et de comprendre les impacts des activités forestières et le rétablissement subséquent des communautés de macroinvertébrés, il est souhaitable d'utiliser simultanément plusieurs descripteurs des communautés, comme l'abondance, la biomasse, la richesse taxonomique et les spectres de taille (Resh *et al.*, 1988; Stone & Wallace, 1998).

Cette étude vise à relier, à quatre échelles spatiales (sous-bassin versant et des rayons d'influence de 8, 2, et 0,5 km en amont des sites), les réponses des communautés de macroinvertébrés aux activités forestières ayant eu lieu de 1 à 19 ans avant l'échantillonnage. Afin d'éviter que la variabilité naturelle ne masque les effets des activités forestières, des variables environnementales caractérisant les ruisseaux ont été mesurées et les caractéristiques du paysage ont été quantifiées pour chacune des échelles étudiées et intégrées dans les analyses. Pour mieux comprendre comment les activités forestières affectent les communautés de macroinvertébrés, la richesse taxonomique raréfiée, la densité numérique et la biomasse, la pente des spectres de biomasse normalisés, la masse médiane et la structure des communautés d'invertébrés ont été utilisés comme indicateurs de la réponse des communautés à ces activités.

MÉTHODES

L'échantillonnage a été réalisé sur 90 seuils répartis dans 22 ruisseaux tributaires (ordre hydrologique 1 à 5) de la rivière Grande Cascapédia, Québec, Canada (Fig. 2.1), entre les mois de juillet et septembre en 2001 et juillet et août 2002 (45 sites chaque année). Cette rivière draine un bassin versant de 3172 km^2.

À chaque site, 18 variables environnementales caractérisant le ruisseau et les berges ont été quantifiées (Tableau 2.1). De plus, 16 variables caractérisant le paysage et les activités forestières ont été quantifiées aux quatre échelles spatiales par SIG (ArcGIS, V. 8.2) en utilisant les cartes écoforestières 1 : 20 000 du Ministère des Ressources naturelles et de la Faune du Québec. Les variables forestières comprenaient la proportion des superficies couvertes par les coupes totales ou partielles pour les classes d'âge de 1, 2-4, 5-9, 10-14 et 15-19 ans, la densité de routes (km km^{-2}) et le nombre d'intersections de routes avec les ruisseaux (nombre km^{-2}).

À chaque site, les macroinvertébrés ont été échantillonnés quantitativement, de manière aléatoire, en période d'étiage à l'aide de filets Surber. Au laboratoire, les macroinvertébrés ont été identifiés jusqu'au genre lorsque possible (Wiggins, 1977; Merritt & Cummins, 1996; Peckarsky et al., 1990; Thorp & Covich, 2001). La longueur des individus a été mesurée de l'extrémité de la tête au bout de l'abdomen, en excluant les cerques et les antennes, à l'aide d'une loupe binoculaire munie d'un micromètre sur un oculaire (précision de 0,01 mm).

Pour chaque site, la richesse taxonomique raréfiée, la densité numérique et la biomasse, la pente des spectres de biomasse normalisés et la masse médiane des organismes ont été mesurées.

La richesse taxonomique est influencée par la taille des échantillons (McCabe & Gottelli, 2000). Nous avons donc utilisé la raréfaction (ECOSIM 7; Gottelli & Entsminger 2004) afin de pouvoir comparer la richesse taxonomique entre les sites puisque le nombre d'individus et l'effort d'échantillonnage pouvaient varier d'un site à l'autre. La masse sèche (MS mg) des individus a été calculée à l'aide d'équations de longueur-masse publiées (Smock, 1980; Towers, Henderson & Veltman, 1994; Hodar, 1996; Benke *et al.*, 1999; Johnston & Cunjak, 1999; Stead *et al.*, 2003). En l'absence d'équations longueur-masse, nous avons utilisé la masse moyenne des individus du taxon. Afin de quantifier les différences des spectres de biomasse normalisés entre les sites et la distribution de la biomasse entre les 13 classes de biomasse (données transformées sous forme logarithmiques) couvrant l'étendue de la masse corporelle des individus des échantillons, la pente des régressions des spectres de biomasse normalisés a été utilisée dans les analyses (Hanson, 1990; Rodríguez & Magnan, 1993; Zimmer *et al.*, 2001).

Des régressions multiples pas à pas avec sélection de variables progressive ont été effectuées (programme SYSTAT, v. 10.2) afin de relier la richesse taxonomique raréfiée, la densité numérique et la biomasse, la pente des spectres de biomasse normalisés et la masse médiane des macroinvertébrés aux activités forestières et aux variables environnementales. Un modèle de régression a été retenu pour chaque variable biologique aux quatre échelles spatiales.

Des analyses canoniques des correspondances (programme CANOCO, v. 4.5; ter Braak & Smilauer, 2002) ont été utilisées pour relier la structure des communautés (abondance relative basée sur la densité numérique) aux activités forestières et aux variables environnementales et ce, pour chacune des quatre échelles spatiales. L'année de l'échantillonnage a été utilisée comme co-variable afin de prendre compte de son influence.

RÉSULTATS

Dans les sites touchés par les coupes récentes (coupes ≤ 4 ans), la richesse diminuait lorsqu'il y avait une augmentation de la proportion de coupes par rapport à l'ensemble des sites (Tableau 2.2) contrairement aux sites touchés par les coupes plus anciennes (coupes ≥ 10 ans), où la richesse augmentait avec l'augmentation de la proportion de coupes. À l'échelle du sous-bassin, une analyse de l'effet net prédit de la proportion de coupes totales d'un an sur la richesse a montré que la richesse diminuait rapidement même avec une faible augmentation de la proportion de coupes (Fig. 2.3).

Par rapport à l'ensemble des sites, la densité numérique augmentait avec une augmentation de la proportion de coupes forestières, qu'elles soient récentes (2-4 ans) ou plus anciennes (≥10 ans, Tableau 2.2).

La biomasse des macroinvertébrés quant à elle augmentait avec les coupes partielles de 5-9 ans à toute les échelles et avec les coupes totales d'un an à l'échelle de 2 km (Tableau 2.2).

La pente des spectres de biomasse était négativement reliée aux coupes, qu'elles soient récentes ou plus anciennes (Tableau 2.2). Par conséquent, dans les sites touchés par les coupes, la taille des organismes avait tendance à diminuer avec l'intensification des coupes forestières par rapport à l'ensemble des sites.

La biomasse médiane des macroinvertébrés était reliée négativement aux coupes récentes (coupes partielles de 1 an), mais seulement à l'échelle de 8 km (Tableau 2.2).

Afin d'approfondir l'examen des relations entre les activités forestières et les variables biotiques, des régressions multiples ont été réalisées pour relier la proportion et la densité de chironomidés aux activités forestières et aux variables environnementales à l'échelle du sous-bassin. Ceux-ci comptaient pour 44,5 % du total des individus, majoritairement des orthocladiinés (66,7 % des chironomidés) et constituaient la majeure partie de la biomasse totale, surtout au niveau des petites classes de taille (Fig. 2.4 a). Dans les sites touchés par les coupes récentes (coupes totales de 1 ans et coupes partielles de 2-4 ans), la proportion et la densité de chironomidés augmentaient lorsqu'il y avait une augmentation de la proportion de coupes par rapport à l'ensemble des sites (Tableau 2.3). À l'échelle du sous-bassin, une analyse de l'effet prédit de la proportion de coupes totales de 1 an (Fig. 2.4 b), puis de la proportion de coupes partielles de 2-4 ans (Fig. 2.4 c), sur la proportion et la densité de chironomidés a montré que la proportion et la densité de chironomidés augmentaient rapidement même avec une faible augmentation des proportions de coupes.

Puisque les modèles finaux pour les ACC étaient similaires à toutes les échelles, seul celui à l'échelle du sous-bassin est présenté (Fig. 2-5 a-d, Tableau 2.4). Deux variables forestières, les coupes totales de 1 an et de 15-19 ans, avaient une forte corrélation avec le premier axe d'ordination, tel qu'indiqué par la longueur des flèches correspondantes dans la figure d'ordination (Fig. 2.5a), et semblaient former un gradient contrastant les coupes récentes et anciennes. Le seul patron évident dans la distribution des principaux groupes taxonomiques concernait les taxons de trichoptère, qui semblaient éviter les sites ayant une forte proportion de coupes totales de 1 an (Fig. 2.5c). La figure d'ordination montrait que seulement 7 des 37 taxons de trichoptères avaient leur maximum d'abondance dans les sites dont le sous-bassin comprenait une grande proportion de coupes totale de 1 an, ce qui contrastait avec la distribution plus homogène

(46 des 101) des taxons qui n'étaient pas des trichoptères (test exact de Fisher, P = 0.005). De plus, les taxons de trichoptères semblaient positivement reliés aux coupes de 15-19 ans (Fig. 2.5c). Une régression multiple additionnelle entre le nombre de taxons total de trichoptères et la proportion de coupes totales de 1 an et de 15-19 ans montrait aussi une relation de la richesse des trichoptères avec les coupes totales d'un an (coefficient partiel standardisé, $b_{1\text{ an}} = 0{,}21$, $p = 0.02$) et de 15-19 ans ($b_{15\text{-}19\text{ ans}} = 0{,}48$, $p< 0.001$). Finalement, la relation positive détectée dans les régressions multiples entre l'abondance des chironomidés et les coupes d'un an n'était pas vraiment apparente à partir de la distribution du maximum d'abondance des taxons de chironomidés dans l'ordination de l'ACC (Fig. 5d).

DISCUSSION

Les influences des coupes sur les macroinvertébrés semblaient se manifester sur une longue période, comme dans d'autres études (Haefner & Wallace 1981; Silbee & Larson, 1983), puisqu'elles ont été détectées jusqu'à 19 ans après qu'elles aient eu lieu. À toutes les échelles, la richesse était reliée aux coupes forestières, mais les relations entre les variables environnementales et la richesse n'ont été détectées qu'à l'échelle de 0,5 km. L'influence des coupes n'a été détectée qu'aux deux plus grandes échelles pour la densité et la pente des spectres de biomasse, seulement à l'échelle de 8 km pour la masse médiane, mais à toutes les échelles pour la biomasse individuelle. Il est possible que l'impact des coupes forestières sur les communautés de macroinvertébrés soit mieux détecté lorsque l'on considère l'ensemble ou une grande partie du bassin. Les effets de chaque parcelle de coupe pourraient s'accumuler sur l'ensemble d'un bassin, tel que suggéré dans certaines études (Murphy *et al.*, 1981; Buttle & Metcalfe, 2000).

Dans une comparaison entre l'impact des inondations dans des ruisseaux désertiques (Fisher *et al.*, 1982) et les coupes à blanc dans les ruisseaux des Appalaches, Gurtz & Wallace (1984) ont trouvé des similitudes dans les caractéristiques de la succession des communautés de macroinvertébrés immédiatement après les perturbations naturelles ou anthropiques. Entre autres, ils ont détecté une dominance des petits organismes généralistes à courte longévité suivant les perturbations. Les organismes polyvoltins généralistes, comme les chironomidés, augmentaient rapidement après les coupes alors que les organismes spécialistes, moins féconds et à développement plus lent, diminuaient (Gurtz & Wallace, 1984).

En accord avec leurs résultats, cette étude montre que la richesse et la taille des organismes diminuaient avec une augmentation de la proportion de coupes récentes (≤ 4 ans), alors que la densité et la biomasse totale augmentaient. Le maximum de l'abondance relative de la majorité des taxons de trichoptères ainsi que la richesse des trichoptères étaient reliés négativement aux coupes totales d'un an. De plus, l'abondance des chironomidés, principalement composés d'individus appartenant à la sous famille des orthocladiinés, lesquels ont généralement un cycle de vie polyvoltin (Tokeshi, 1995), augmentait avec l'accroissement de la proportion de coupes récentes. Les chironomidés représentaient la majeure proportion des petits organismes en termes de densité et de biomasse.

Alors que la richesse diminuait dans les zones récemment coupées, elle était positivement reliée aux coupes plus anciennes (10-19 ans). Les trichoptères semblaient également être positivement reliés aux coupes totales plus anciennes (15-19 ans). Ceci suggère qu'il y a eu rémission des communautés d'invertébrés et de la condition des ruisseaux après quelques années. Cette dernière est étroitement reliée au processus de régénération de la forêt (Stone & Wallace, 1998) et à la formation d'amoncellement de débris dans les petits ruisseaux (Yount & Niemi, 1990), et peut être décalée par rapport au rétablissement des parties terrestres du bassin (Gurtz & Wallace, 1984).

La capacité à détecter les relations entre les coupes forestières et les communautés d'invertébrés dépendait des variables biotiques utilisées. De plus, ces relations ont été observées en tenant compte du contexte environnemental, qui aurait pu autrement masquer l'effet des coupes forestières. La réponse des variables biotiques aux coupes forestières variait selon l'échelle d'observation et elle était généralement plus forte aux plus grandes échelles, ce qui suggère que les effets des activités forestières pourraient s'additionner tout le long des cours d'eau (Allan, 2004). Ces effets pourraient être exportés des petits ruisseaux à forte pente, pour s'accumuler dans les seuils à plus faible pente des plus grands ruisseaux, et ainsi perturber les communautés de macroinvertébrés en aval (Murphy *et al.*, 1981; Buttle & Metcalfe, 2000).

La réponse générale des communautés aux coupes récentes était une diminution de la richesse taxonomique, particulièrement celle des trichoptères, et de la taille des individus alors que la densité et la biomasse augmentaient, tout comme la densité et la proportion de chironomidés. La majorité des taxons de trichoptères étaient également reliés négativement aux coupes récentes. Ceci suggère que certains taxons, peut-être davantage spécialisés et à long cycle vital, peuvent avoir été remplacés par des macroinvertébrés généralistes, plus petits et à cycle polyvoltin comme les orthocadiinés et d'autres chironomidés. Ces changements pourraient avoir des conséquences sur les organismes de niveaux trophiques supérieurs, comme les poissons, qui se nourrissent d'invertébrés, si leurs proies favorites ou de taille optimale pour eux deviennent moins disponibles (Poff & Huryn, 1998). Ces relations entre les coupes forestières et les variables biotiques ont été observées malgré la présence de bandes riveraines le long des berges des cours d'eau étudiés. Il semble donc que ces lisières boisées d'une largeur de 20 m ne soient pas suffisantes pour atténuer complètement les effets des activités forestières sur l'écosystème aquatique.

Dans les études observationnelles, les influences environnementales peuvent être contrôlées statistiquement afin de faciliter la détection des impacts des activités forestières. Dans cette étude, les effets des activités forestières sur les macroinvertébrés ont été détectés après avoir tenu compte de la variabilité environnementale naturelle, qui autrement aurait pu masquer ces effets. L'examen de l'effet prédit partiel des coupes forestières s'est révélé fructueux dans la présente étude, par exemple, en faisant ressortir que la richesse peut diminuer rapidement en réponse aux coupes, même si seulement de petites portions de bassins sont touchées (Kiffney *et al.*, 2003). L'utilisation de plusieurs variables biotiques et des techniques d'analyses partielles pour examiner les effets des activités forestières sur les macroinvertébrés à plusieurs échelles spatiales pourraient s'avérer une approche très prometteuse pour faciliter l'interprétation des résultats et mieux comprendre l'effet des coupes dans les études à venir.

Chapitre 2. Response of stream macrobenthos to forestry activities and environmental context at multiple spatial scales

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SUMMARY

1. Responses of stream macrobenthic communities to forestry activities at four spatial scales (sub-basin, and 8-, 2-, and 0.5-km influence 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.

2. Multiple regression models and canonical correspondence analysis were used to relate six biological metrics: taxonomic richness, numerical density, biomass density, normalized biomass spectrum, individual body mass, and community structure, to variables quantifying logging 1-19 years prior to the study and road density. Environmental predictors were included in all analyses to statistically account for environmental context and increase the likelihood of detecting potentially subtle forestry impacts.

3. Logging activities were linked to decline in taxonomic richness, increase in numerical and biomass densities, and shift in size structure of benthic macroinvertebrates at the largest (sub-basin and 8-km) scales, 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.

4. These changes reflected primarily marked increases in the abundance of chironomids, and decline in the number of trichopteran taxa, with increasing areal coverage of recent ($\leq$2-4 yr) cuts, suggesting that larger, longer-lived and possibly more specialized 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 at very low values (<1%) of 1 yr clear-cuts.

5. 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 and partialling, at multiple spatial scales, may be a broadly applicable approach for enhancing sensitivity and facilitating interpretation in studies of anthropogenic effects on macroinvertebrate communities.

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 & Joensu, 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; Hynes, 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 *et al.*, 1980; Noel *et al.*, 1986; Kreutzweiser, Capell & Good, 2005). 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 pathways and mechanisms 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, but 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 gradient and transport capacity, 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, positive responses to logging were detected more often for taxa on large, more physically stable substrata, whereas negative responses were more common for taxa 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 appeared to be more sensitive indicators of long-term recovery than those in moss-covered bedrock (Stone & Wallace, 1998).

Clearly, environmental context should be considered when evaluating forestry impacts; otherwise, natural environmental variation among sites may mask such impacts. In observational studies that examine variation across multiple sites in a survey, statistical tools such as partialling, which enables one to isolate the effect of a variable by holding constant or controlling, by statistical means, the effects of all other variables included in the analysis, can facilitate detection of the effects of interest (Rodríguez & Magnan, 1995).

The present study examines the responses of stream macrobenthic communities to forestry activities occurring 1-19 years prior to the study, at four spatial scales (sub-basin, and 8-, 2-, and 0.5-km radii upstream of study sites). Because different characterizations of benthic communities, such as the biomass spectrum and community structure, can emphasize strikingly different aspects of ecological processes (Rodríguez & Magnan, 1993), use 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). Therefore, six different biological metrics, taxonomic richness, numerical density, biomass density, normalized biomass spectrum, individual body mass, and community structure, were used to assess the responses of macrobenthic communities to forestry activities. 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 (Fig. 1), 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 stream transects drawn 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), by hand-scrubbing rocks (4-6 min) 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 for subsequent identification in the laboratory 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; Towers, Henderson & Veltman, 1994; Hodar, 1996; Benke *et al.*, 1999; Johnston & Cunjak, 1999; Stead *et al.*, 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 were 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. Wetted width was measured at each transect. Water temperature was measured at the center of the middle transect (hand-held thermometer). Mean substratum size (modified Wentworth scale) was 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 center of the stream) and slope over the stream reach were measured with a hand-held clinometer (PM-5, Suunto, Vantaa, Finland). The height increment and width 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 1:20000 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) was used to quantify landscape features and forestry activities at four spatial scales: sub-basin, and 8-, 2-, and 0.5-km influence radii upstream of each site (Fig. 2). The landscape variables were stream gradient (mean slope from site to end of the influence zone), area of the upstream influence zones (ha), and percent areal coverage of conifers and of deciduous vegetation. Logging activities were grouped into two categories reflecting the harvesting procedures employed: 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 (percent 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 yr), and the density of roads (km km^{-2}) and of road junctions with streams (junctions km^{-2}).

Sampling year was included as an independent variable to account for possible interannual differences. Separate multiple regressions were used to relate five biological metrics, rarefied taxonomic richness, numerical and biomass densities, slope of the normalized biomass spectra, and median individual mass, to environmental and forestry variables (Table 1). 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; cutoff for variable entry or removal at $P \leq 0.05$) was used to determine which predictors to retain in the final regression models (program SYSTAT, v. 10.2; SPSS Inc., 2002). The tolerance (Tabachnick & Fidell, 2000) for predictors in final models always exceeded 0.65, indicating only mild collinearity among predictors. To account for differences in abundance among sites (range: 74-4978 individuals), taxonomic richness was obtained by rarefaction (mean of 1000 trials, program Ecosim v. 7; Gotelli & Entsminger, 2004). To characterize 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 $\leq$0.08 mg DM and class 13 corresponding to body mass $\geq$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. Normalized 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 biomass 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 (cutoff $P = 0.05$) 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. Significance values for individual variables and for the sum of all eigenvalues was 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 yr 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 yr) to older (≥10 yr) cuts, as indicated by the opposite signs of standardized coefficients for recent and older cuts. After partialling out statistically the influence of other variables, richness showed nonlinear decline with increases in 1 yr clear-cuts, with the most rapid change occurring at the lowest values (<1%) of clear-cuts (Fig. 3). At all scales, richness declined over the summer. The amount of variation 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, across 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, (2-4 yr and 15-19 yr partial cuts), but only at the largest 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 5-9 yr partial cuts at all scales, and with 1 yr clear-cuts at the 2-km scale.

The slope of the normalized 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 yr) or older (15-19 yr) 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; 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 yr 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 (Appendix 1). 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 4a). 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 yr clear-cuts and 2-4 yr partial cuts (Table 3). The models indicated that after partialling out statistically the environmental effects, the most rapid change in both proportion and density occurred at very low (<1%) values of percentage cover for both 1 yr clear-cuts (Fig. 4b) and 2-4 yr partial cuts (Fig. 4c).

Final CCA models were broadly similar at all spatial scales; therefore, results are presented only for the sub-basin scale (Fig. 5a-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. 5a, b). Two forestry variables, 1 yr clear-cuts and 15-19 yr clear-cuts, had high correlations with the first ordination axis and appeared to define a gradient contrasting old and recent cuts (Fig. 5a). 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 yr clear-cuts (Fig. 5c). The ordination plot indicates that only 7 of 37 trichopteran taxa had peak modal abundance in sites with a high proportion of 1 yr 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 of trichopteran taxa on the proportions of 1 yr and 15-19 yr clear-cuts for the 90 riffle sites also pointed to an association of trichopteran richness with 1 yr clear-cuts (partial standardized coefficient, $b_{1\ \mathrm{yr}} = -0.21$, $P = 0.02$) and 15-19 yr clear-cuts ($b_{15\text{-}19\ \mathrm{yr}} = 0.48$, P

< 0.001). The positive relationship previously detected in the multiple regression analyses between chironomid abundance and 1 yr clear-cuts was not readily apparent from the distribution of peak modal abundances of chironomid taxa in the CCA ordination (Fig. 5d).

DISCUSSION

The main finding of this study is that logging activities were linked 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 reflected primarily 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 specialized taxa, in particular trichopterans, were more vulnerable to forestry impacts and were replaced at recently-logged sites by smaller, multivoltine, generalist 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 specialized organisms, and allow a few successful species to become dominant, 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 specialized feeding, and slower development (Gurtz & Wallace, 1984). Shifts in the size structure and taxonomic composition of invertebrate prey resulting from logging 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 yr) cuts, but seemed favoured by older (10-19 yr) 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 across 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 be 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 *et al.*, 2003; Kiffney *et al.*, 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-m or 60-m buffer strips and the only apparent influence of canopy opening was a small negative effect on taxonomic richness at the 0.5-km scale. 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 which may have otherwise concealed those effects. The examination of predicted forestry effects with environmental influences held constant by partialling 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 use of multiple biological metrics and partialling techniques 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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TABLE 2.1. 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	Interquartile range	Range
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 normalized 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)

TABLE 2.1. (continued and concluded).

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 at flood (m)	2.7	(2.0, 4.0)	(0.4, 22.4)

TABLE 2.2. Standardized 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 normalized 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 Variable name	Spatial scale (influence radii)			
	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 yr clear-cuts	-0.384 (<0.001)	-0.266 (0.002)	-0.171 (0.040)	-0.184 (0.030)
% 2-4 yr partial cuts	-0.305 (0.003)			
% 10-14 yr partial cuts	0.318 (0.002)	0.390 (<0.001)		
% 15-19 yr clear-cuts			0.491 (<0.001)	0.407 (<0.001)
% 15-19 yr 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)

TABLE 2.2. (continued).

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)
% 2-4 yr partial cuts	0.395 (<0.001)	0.262 (0.004)		
% 15-19 yr 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 yr clear-cuts			0.164 (<0.001)	
% 5-9 yr 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

TABLE 2.2. (continued and concluded).

Slope of normalized 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)
% 2-4 yr clear-cuts	-0.192 (0.037)	-0.258 (0.005)		
% 2-4 yr partial cuts	-0.391 (<0.001)	-0.328 (<0.001)		
% 15-19 yr 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 yr partial cuts		-0.218 (0.005)		
R^2	0.556	0.568	0.556	0.556

TABLE 2.3. Standardized 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	Standardized 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 yr clear-cuts	0.301 (<0.001)
	% 2-4 yr 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 yr clear-cuts	0.245 (0.002)
	% 2-4 yr partial cuts	0.364 (<0.001)
	R^2	0.596

TABLE 2.4. 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

FIGURE CAPTIONS

FIGURE 2.1. Location of the 90 study sites (circles) distributed among 22 tributary streams in the Cascapedia River basin, Québec, Canada.

FIGURE 2.2. Schematic representation of zones of influence 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.

FIGURE 2.3. Conditional relationship between the rarefied taxonomic richness and the proportion of 1 yr clear-cuts at the sub-basin scale. Predicted values were obtained from the multiple regression model for rarefied taxonomic richness, by fixing all independent variables other than 1 yr clear-cuts at their means.

FIGURE 2.4. 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 yr 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 2-4 yr 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 yr or 2-4 yr clear-cuts at their means.

FIGURE 2.5. CCA 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 yr clear-cuts, indicating negative association with 1 yr 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).

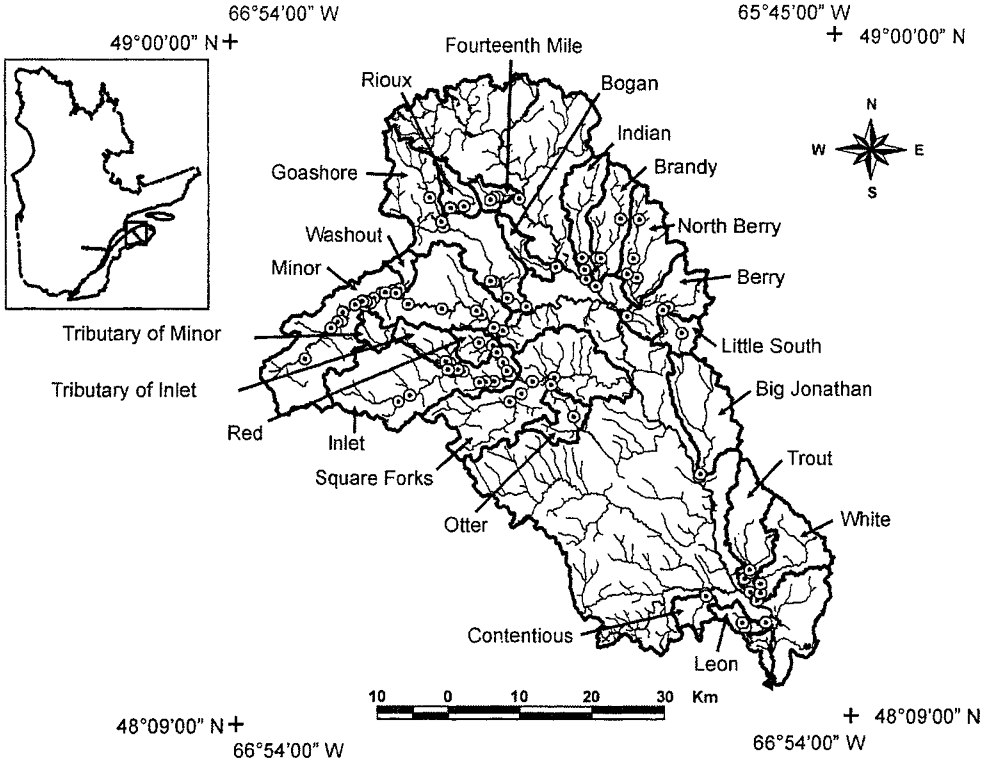

FIGURE 2.1.

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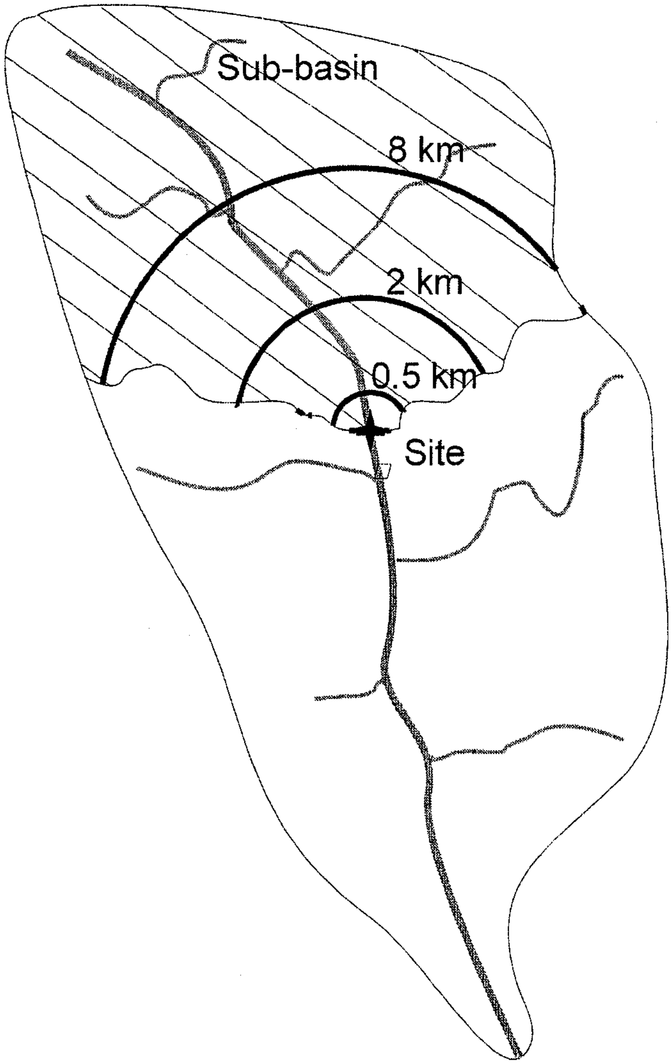

FIGURE 2.2.

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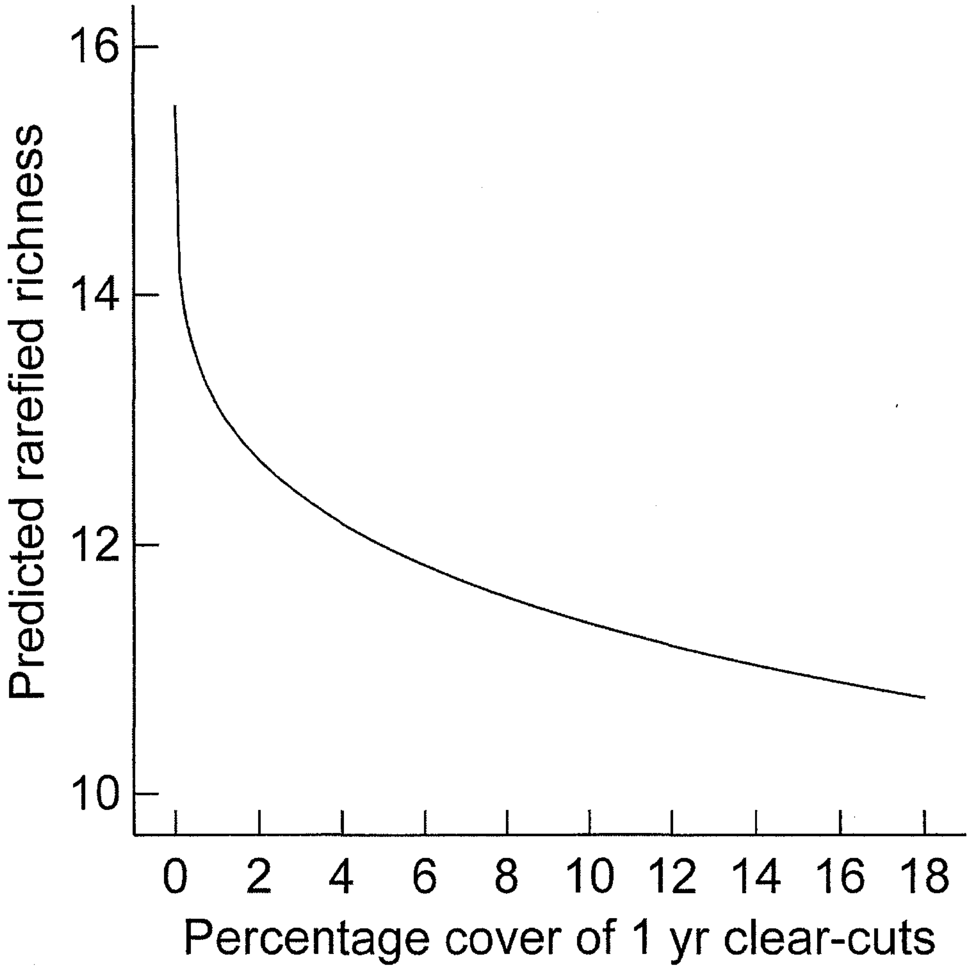

FIGURE 2.3.

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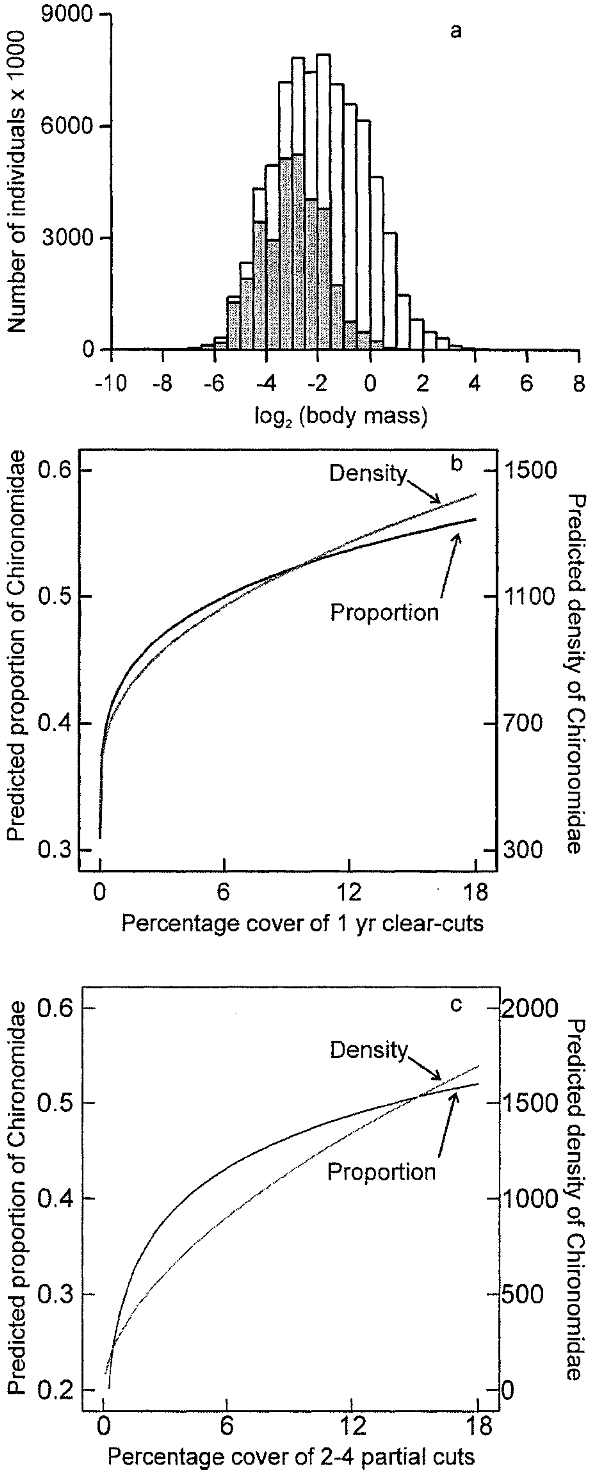

FIGURE 2.4.

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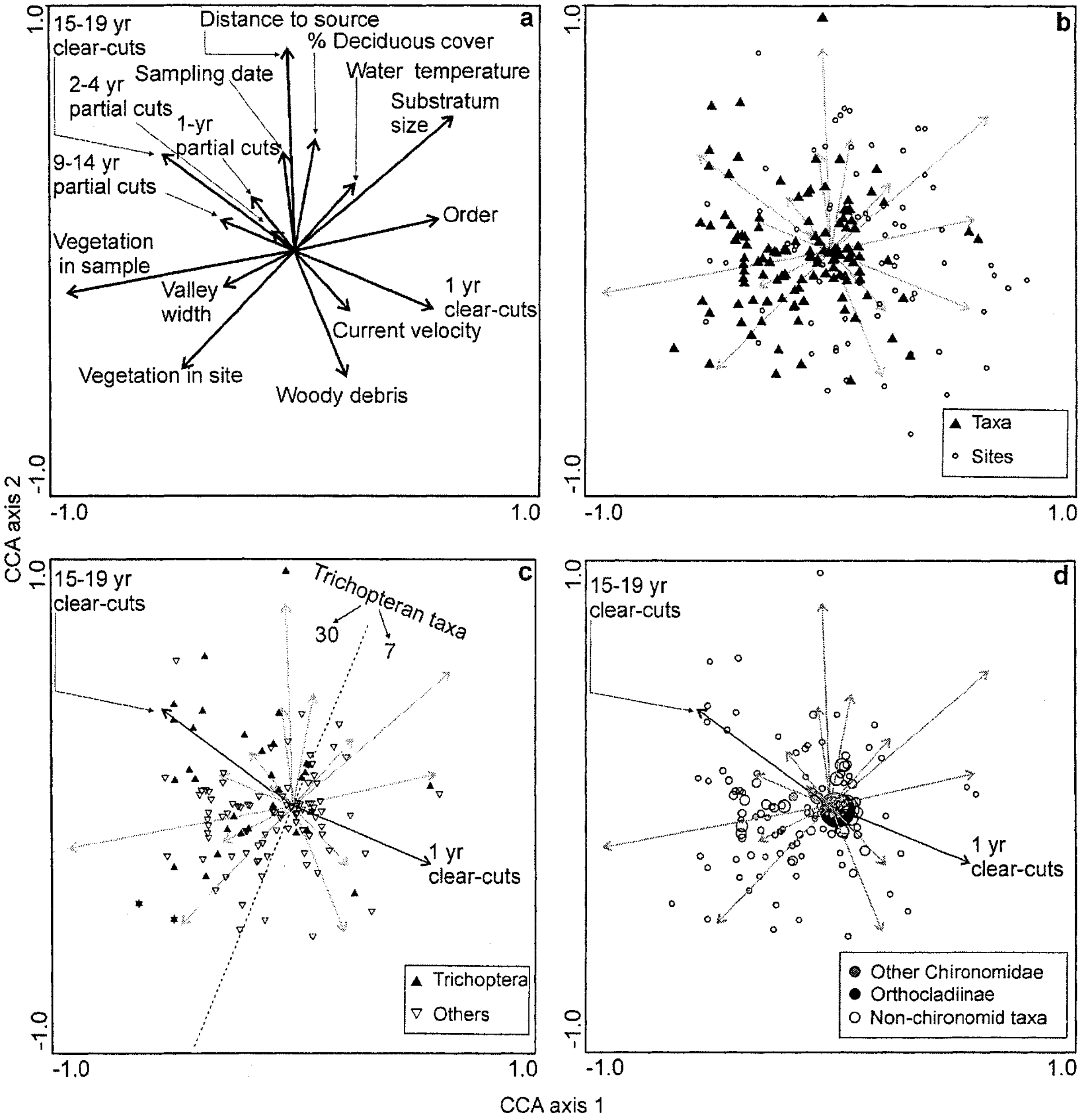

FIGURE 2.5.

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APPENDIX 1. Number of organisms collected, median density (number m^{-2}) and interquartile range (IR, in parenthesis), and occurrence by sites (N= 90) and streams (N = 22), for 137 macroinvertebrate taxa. The total number of organisms is 78321.

Taxon	Number	Median density (number m^{-2})	IR	Occurrence	
				Sites	Streams
Bivalvia					
Sphaeridae	65	0.0	(0.0, 0.0)	10	2
Collembola	11	0.0	(0.0, 0.0)	9	7
Entomobryidae	11	0.0	(0.0, 0.0)	8	7
Hypogastruridae	1	0.0	(0.0, 0.0)	1	1
Isotomidae	2	0.0	(0.0, 0.0)	2	2
Semicerura sp.	3	0.0	(0.0, 0.0)	1	1
Sminthuridae	4	0.0	(0.0, 0.0)	4	3
Sminthurides sp.	16	0.0	(0.0, 0.0)	9	6
Hydrachnida	1872	39.5	(15.2, 73.1)	85	22
Nematoda	4	0.0	(0.0, 0.0)	3	2
Oligochaeta	249	0.0	(0.0, 0.0)	21	15
Aeolosomatidae	13	0.0	(0.0, 0.0)	2	1
Enchytraeidae	6	0.0	(0.0, 0.0)	1	1
Lumbricidae	110	0.0	(0.0, 1.8)	25	14
Naïdidae	457	0.0	(0.0, 1.8)	25	17

APPENDIX 1 (continued).

Turbellaria					
Planariidae	485	9.0	(3.6, 21.5)	75	22
Coleoptera	11	0.0	(0.0, 0.0)	3	2
Elmidae	3	0.0	(0.0, 0.0)	2	1
Promoresia sp.	5	0.0	(0.0, 0.0)	3	1
Georyssidae	1	0.0	(0.0, 0.0)	1	1
Diptera	54	0.0	(0.0, 0.0)	11	5
Athericidae					
Atherix sp.	243	0.0	(0.0, 7.2)	42	16
Blephariceridae	33	0.0	(0.0, 0.0)	6	3
Ceratopogonidae	3	0.0	(0.0, 0.0)	3	2
Forcipomyia sp.	1	0.0	(0.0, 0.0)	1	1
Chironomidae	38	0.0	(0.0, 0.0)	5	4
Chironomini sp.	158	0.0	(0.0, 2.6)	29	12
Tanytarsini sp.	10264	87.0	(32.3, 276.7)	87	22
Orthocladiinae	23232	538.2	(121.1, 1016.8)	90	22
Tanypodinae	1140	6.3	(0.0, 43.1)	64	19
Dixidae	6	0.0	(0.0, 0.0)	5	3
Empididae	8	0.0	(0.0, 0.0)	3	2
Chelifera sp.	275	5.4	(0.0, 13.9)	64	20
Clinocera sp.	2	0.0	(0.0, 0.0)	1	1

APPENDIX 1 (continued).

Hemerodromia sp.	87	0.0	(0.0, 3.6)	35	12
Oreogeton sp.	4	0.0	(0.0, 0.0)	3	3
Muscidae					
Limnophora sp.	23	0.0	(0.0, 0.0)	7	7
Psychodidae	1	0.0	(0.0, 0.0)	1	1
Psychoda sp.	3	0.0	(0.0, 0.0)	2	2
Ptychopteridae	4	0.0	(0.0, 0.0)	1	1
Simuliidae	31	0.0	(0.0, 0.0)	9	3
Prosimulium sp.	288	0.0	(0.0, 0.0)	13	2
Simulium sp.	7663	43.1	(14.4, 191.1)	82	22
Stratiomyidae					
Odontomyia sp.	2	0.0	(0.0, 0.0)	1	1
Tabanidae	2	0.0	(0.0, 0.0)	1	1
Tipulidae	92	0.0	(0.0, 3.6)	31	19
Tipula sp.	4	0.0	(0.0, 0.0)	2	2
Limoniinae	2	0.0	(0.0, 0.0)	1	1
Antocha sp.	24	0.0	(0.0, 0.0)	10	4
Cryptolabis sp.	6	0.0	(0.0, 0.0)	2	2
Hexatoma sp.	4	0.0	(0.0, 0.0)	4	3
Limnophila sp.	2	0.0	(0.0, 0.0)	2	1
Ephemeroptera	1243	0.0	(0.0, 4.9)	25	13

APPENDIX 1 (continued).

Ameletidae					
Ameletus sp.	1	0.0	(0.0, 0.0)	1	1
Baetidae	179	0.0	(0.0, 0.0)	20	8
Acentrella sp.	256	0.0	(0.0, 0.0)	13	3
Acerpenna sp.	238	0.0	(0.0, 0.0)	12	2
Baetis sp.	7995	141.7	(44.0, 297.4)	84	22
Procleon sp.	22	0.0	(0.0, 0.0)	2	2
Ephemerellidae	384	0.0	(0.0, 0.0)	16	6
Attenella sp.	1	0.0	(0.0, 0.0)	1	1
Drunella sp.	648	7.2	(0.0, 30.1)	56	14
Ephemerella sp.	2926	25.5	(7.2, 84.8)	78	22
Timpanoga sp.	1	0.0	(0.0, 0.0)	1	1
Heptageniidae	100	0.0	(0.0, 0.0)	19	7
Cinygmula sp.	691	7.2	(0.0, 21.5)	57	19
Epeorus sp.	2935	50.2	(8.1, 111.2)	74	21
Heptagenia sp.	42	0.0	(0.0, 0.0)	17	3
Rhithrogena sp.	306	0.0	(0.0, 10.3)	39	15
Stenonema sp.	1	0.0	(0.0, 0.0)	1	1
Leptophlebiidae	36	0.0	(0.0, 0.0)	10	2
Habrophlebiodes sp.	571	3.6	(0.0, 17.9)	52	17
Leptophlebia sp.	9	0.0	(0.0, 0.0)	1	1

APPENDIX 1 (continued).

Paraleptophlebia sp.	72	0.0	(0.0, 0.0)	12	2
Siphlonuridae	2	0.0	(0.0, 0.0)	1	1
Hemiptera	8	0.0	(0.0, 0.0)	7	3
Belostomatidae					
Belostoma sp.	2	0.0	(0.0, 0.0)	2	2
Lepidoptera	10	0.0	(0.0, 0.0)	9	7
Megaloptera					
Sialidae					
Sialis sp.	6	0.0	(0.0, 0.0)	5	5
Plecoptera	500	0.0	(0.0, 0.0)	21	14
Capniidae	5	0.0	(0.0, 0.0)	1	1
Chloroperlidae	123	0.0	(0.0, 0.0)	15	10
Alloperla sp.	3	0.0	(0.0, 0.0)	2	2
Haploperla sp.	4	0.0	(0.0, 0.0)	2	2
Suwallia sp.	4	0.0	(0.0, 0.0)	4	1
Sweltsa sp.	63	0.0	(0.0, 0.0)	15	4
Utaperla sp.	1178	23.3	(7.2, 44.4)	75	22
Suwallia sp.	4	0.0	(0.0, 0.0)	4	1
Leuctridae	110	0.0	(0.0, 0.0)	21	13
Leuctra sp.	1420	13.0	(3.6, 76.7)	74	22
Nemouridae	15	0.0	(0.0, 0.0)	3	2

APPENDIX 1 (continued).

Amphinemura sp.	6	0.0	(0.0, 0.0)	4	3
Zapada sp.	228	0.0	(0.0, 3.6)	36	19
Perlodidae	252	0.0	(0.0, 1.8)	24	15
Isoperla sp.	13	0.0	(0.0, 0.0)	2	2
Yugus sp.	1	0.0	(0.0, 0.0)	1	1
Pteronarcyidae					
Pteronarcys sp.	15	0.0	(0.0, 0.0)	9	3
Taeniopterygidae					
Taeniopteryx sp.	2	0.0	(0.0, 0.0)	1	1
Trichoptera	109	0.0	(0.0, 5.3)	39	19
Apataniidae					
Apatania sp.	58	0.0	(0.0, 0.0)	9	2
Brachycentridae	7	0.0	(0.0, 0.0)	3	2
Brachycentrus sp.	2133	23.3	(0.0, 78.5)	55	14
Glossosomatidae	20	0.0	(0.0, 0.0)	4	4
Agapetus sp.	2	0.0	(0.0, 0.0)	2	1
Glossosoma sp.	2235	21.5	(0.0, 94.8)	64	18
Goeridae					
Goera sp.	1	0.0	(0.0, 0.0)	1	1
Hydroptilidae	12	0.0	(0.0, 0.0)	3	2
Hydroptila sp.	1060	0.0	(0.0, 12.6)	38	12

APPENDIX 1 (continued).

Ochrotrichia sp.	9	0.0	(0.0, 0.0)	2	1
Oxyethira sp.	45	0.0	(0.0, 0.0)	4	3
Hydropsychidae	13	0.0	(0.0, 0.0)	7	2
Arctopsyche sp.	4	0.0	(0.0, 0.0)	2	1
Ceratopsyche sp.	1	0.0	(0.0, 0.0)	1	1
Hydropsyche sp.	147	0.0	(0.0, 1.2)	23	5
Parapsyche sp.	8	0.0	(0.0, 0.0)	1	1
Lepidostomatidae	2	0.0	(0.0, 0.0)	1	1
Lepidostoma sp.	12	0.0	(0.0, 0.0)	5	1
Leptoceridae	2	0.0	(0.0, 0.0)	1	1
Ceraclea sp.	5	0.0	(0.0, 0.0)	2	1
Leptocerus sp.	2	0.0	(0.0, 0.0)	1	1
Mystacides sp.	1	0.0	(0.0, 0.0)	1	1
Limnephilidae	584	7.9	(0.0, 19.0)	58	18
Ecclisomyia sp.	3	0.0	(0.0, 0.0)	1	1
Homophylax sp.	4	0.0	(0.0, 0.0)	1	1
Limnephilius sp.	3	0.0	(0.0, 0.0)	3	3
Platycentropus sp.	1	0.0	(0.0, 0.0)	1	1
Psychoglypha sp.	1	0.0	(0.0, 0.0)	1	1
Pycnopsyche sp.	4	0.0	(0.0, 0.0)	4	1
Philopotamidae	300	0.0	(0.0, 0.0)	19	11

APPENDIX 1 (continued and concluded).

Dolophilodes sp.	317	0.0	(0.0, 10.8)	38	13
Wormaldia sp.	2	0.0	(0.0, 0.0)	1	1
Psychomyiidae	3	0.0	(0.0, 0.0)	1	1
Rhyacophilidae	10	0.0	(0.0, 0.0)	5	2
Rhyacophila sp.	1484	21.5	(7.2, 64.6)	78	22
Uenoidae					
Neophylax sp.	54	0.0	(0.0, 0.0)	10	1