Disturbances structuring macroinvertebrate communities in steep headwater streams: relative importance of forest clearcutting and debris flow occurrence

Sohei Kobayashi, Takashi Gomi, Roy C. Sidle, and Yasuhiro Takemon

Abstract: This study shows that debris flow disturbances that alter in-channel physical conditions or displace organisms exert greater impacts on stream macroinvertebrate community structure than clearcutting disturbances that change energy inputs in steep headwater systems. We surveyed abiotic characteristics and macroinvertebrate communities of 10 steep headwater streams in central Japan that contained a chronosequence of forest stands and debris flow occurrences. Streams of recently logged forests had higher light levels, nitrate concentrations, and stream temperature ranges than streams of mature forests. Streams of middle-aged forests, which experienced debris flows in recent years (1989–1998), had lower abundance of shredders, crawlers, and headwater-adapted taxa than the other streams. A shredder taxon, *Gammarus nipponensis*, was completely absent in the streams with recent debris flows, despite their dominance in the other streams. Decreases of depositional environment associated with depletion of large wood and loss of channel structure as well as replacement of community members by rapid colonizers appear to be the major mechanisms of structural changes in macroinvertebrate communities affected by debris flows.

Résumé : Notre étude démontre que les perturbations dues aux coulées de débris qui altèrent les conditions physiques du chenal ou qui délogent les organismes ont un impact plus sévère sur la structure des communautés de macroinvertébrés lotiques que les perturbations dues à la coupe à blanc qui modifient les apports énergétiques dans les systèmes hydrographiques d'amont à forte dénivellation. Nous avons inventorié les conditions abiotiques et les communautés de macroinvertébrés dans 10 cours d'eau d'amont à forte pente du centre du Japon qui possèdent une série chronologique de types de forêts et qui ont connu des événements de coulées de débris. Les cours d'eau dans les forêts récemment coupées ont des intensités lumineuses, des concentrations de nitrates et des étendues de température plus grandes que celles des cours d'eau des forêts matures. Les cours d'eau des forêts d'âge moyen qui ont connu des coulées de débris au cours d'années récentes (1989–1998) contiennent une abondance plus faible de déchiqueteurs, d'organismes rampants et de taxons adaptés aux cours d'eau d'amont que les autres cours d'eau. Un taxon de déchiqueteurs, *Gammarus nipponensis*, fait complètement défaut dans les cours d'eau qui ont subi des coulées de débris récentes, même s'il est dominant dans les autres cours d'eau. La réduction de l'environnement sédimentaire associée à la perte des grands débris ligneux et la destruction de la structure du chenal, ainsi que le remplacement des organismes de la communauté par des espèces à colonisation rapide, semblent constituer les mécanismes principaux des changements dans les communautés de macroinvertébrés benthiques affectées par les flux de débris.

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Introduction

Forest clearcutting and debris flows are major disturbances that affect stream ecosystems in steep, forested catchments. Although these disturbances often occur in the same catchment, their individual and combined effects on aquatic environment have not been clarified in past investigations. Clearcutting affects stream ecosystems because removal of vegetation modifies ecological links between streams and the surrounding environment, especially in headwater catchments (Vannote et al. 1980; Gomi et al. 2002; Richardson et al. 2005). Loss of canopy over the channels and increases of

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solar radiation inputs often result in increased primary production (Webster et al. 1983; Bilby and Bisson 1992; Hill et al. 1995) and stream temperature (Beschta et al. 1987; Johnson and Jones 2000; Moore et al. 2005a). Loss of riparian vegetation also results in decreased organic matter inputs to streams (Webster et al. 1983; Bilby and Bisson 1992). Following clearcutting, benthic invertebrates typically shift from detritivore- to grazer-dominated communities due to changes in the trophic base from allochthonous to autochthonous (Webster et al. 1983; Nislow and Lowe 2006) and increase in abundance and production (Newbold et al. 1980; Stone and Wallace 1998).

Debris flows are mass movements of water and sediment in headwater channels of mountainous regions (Sidle and Ochiai 2006). The scour, transport, and deposition of sediment associated with debris flows substantially damage and displace organisms (Lamberti et al. 1991; Kiffney et al. 2004; Snyder and Johnson 2006) and modify in-channel and riparian physical environments (Swanson et al. 1998; Nakamura et al. 2000; Bilby et al. 2003). Debris flows often expose bedrock by removing sediment and large woody debris and thus reduce roughness in steep channels (Gomi et al. 2003; May and Gresswell 2003). Decreases in channel roughness can result in less slow-flow habitat and more fast-flow habitat for organisms (Bilby et al. 2003) and may reduce accumulated litter, which represents important invertebrate microhabitat in headwater streams (Casas 1997; Kobayashi and Kagaya 2002). In contrast with these negative impacts in headwater streams, debris flows provide sediment and increase habitat heterogeneity for invertebrates over long time scales in downstream reaches (Benda et al. 2003; Bilby et al. 2003).

In managed forests on steep hillslopes, the spatial and temporal patterns of debris flows can be closely related to clearcutting. The probability of landslide occurrence increases 3 to about 15 years after clearcutting associated with deteriorating root strength prior to sufficient vegetation recovery on hillslopes (O'Loughlin and Ziemer 1982; Sidle 1992; Wu and Sidle 1995). Landslides on hillslopes that travel to headwater channels are transformed into channelized debris flows through the accumulation of water, either directly or during future storms (Imaizumi and Sidle 2007; Imaizumi et al. 2008). Although the impacts of clearcutting and debris flows on stream ecosystems are widely recognized, previous studies have not assessed and compared these interrelated impacts on invertebrate communities.

We investigated stream abiotic characteristics and macroinvertebrate communities in steep headwater catchments with different legacies of forest clearcutting and debris flow occurrence. The unique chronosequence of forest stands and debris flow occurrences at our study site in Nara Prefecture, Japan, enabled us to evaluate the responses and recoveries of stream ecosystems to clearcutting and debris flows. We analyzed (i) the relative importance of clearcutting and debris flow occurrence in macroinvertebrate community structure, (ii) possible mechanisms by which these disturbances influence macroinvertebrate communities, and (iii) distribution patterns of macroinvertebrates, both specific to and nonspecific to headwaters, among headwater streams subjected to disturbances.

Materials and methods

Study site

The study was conducted in a mountainous watershed (8.5 km², 860–1370 m above sea level) in the central Kii Peninsula, Japan (34°04′N, 135°35′E) (Fig. 1). The area is upstream of Kanno River within the Kumano River basin (2360 km²). Surficial geology in the area consists of alternating beds of sandstone and shale or mudstone. Hillslopes are steep (~40° mean gradient) with thin surface soils (generally <1 m in deep). Annual precipitation in the area ranged from 2122 to 3508 mm during 1998–2002. Forests of entire individual subwatersheds have been clearcut and planted, predominantly with Japanese cedar (*Cryptomeria japonica*), since 1912. Forest clearcutting generally occurs in early summer followed by timber removal in summer and autumn and replanting in the following spring. Skyline harvesting, in which logs on hillslopes are transported above ground by wire cable to landing areas, has been used in this steep terrain at least since the 1940s. Stands are typically thinned by cutting approximately 25% of the trees about 30 years after planting. Thinned logs are left on site. All forest management entries were conducted either within the context of individual small headwater catchments or within adjoining catchments. In subsequent years, these harvest activities have rotated within the larger watershed. Consequently, the watershed comprises a mosaic of headwater catchments with stand ages ranging from 1 to 91 years (in 2005). Water chemistry and landslide occurrences in the watershed have been reported by Fukushima and Tokuchi (2008) and Imaizumi et al. (2008), respectively.

Nine headwater catchments with a sequence of stand ages (corresponding to time since clearcut logging of 1, 2, 16, 18, 28, 31, 42, 91, and 91 years) were selected in the watershed (Fig. 1). Catchments were identified by stand age (e.g., MF18 indicates an 18-year-old managed forest). During the study period, no major forest operations occurred except in one of the two MF91 catchments where clearcutting began in June 2005. Hereafter, MF91a and MF91b refer to the catchments without and with clearcutting during the study period, respectively. The drainage areas of the nine catchments ranged from 2.5 to 9.0 ha (Table 1). Forest roads cross near the uppermost ridge and downstream of the study catchments, paralleling the Kanno River. Catchments MF1, MF16, MF28, MF31, and MF91b are oriented southeast, whereas catchments MF2, MF18, MF42, and MF91a are oriented northwest or northeast. One undisturbed forest catchment (7.7 ha, facing southeast) located within Kyoto University Wakayama Experimental Forest (2.7 km west of the managed watershed) was selected as a reference site (hereafter called UF). This catchment was covered by a mixture of conifer and deciduous trees dominated by Japanese fir (*Abies firma*) and southern Japanese hemlock (*Tsuga sieboldii*). In this study, we refer to MF1 and MF2 as "recently logged forests", MF16, MF18, MF28, and MF31 as "middle-aged forests", and MF42, MF91a, MF91b, and UF as "mature forests". This classification is not intended to make treatments among catchments a priori but to show patterns among the 10 catchments in a simpler manner.

We identified occurrences of debris flows in the 10 headwater streams using aerial photographs taken in 1948, 1964,

Fig. 1. Site map and photographs of the study site. (*a*) Map of the study site showing the nine managed forest catchments (MF*x*, where *x* indicates stand age (years) in the catchments). An undisturbed forest catchment (UF) was located 2.0 km west of this area. Photographs show (*b*) first-order valleys (headwater streams) that flow into the main Kanno-gawa River, (*c*) one of the recently logged catchments, (*d*) one of the middle-aged forest catchments with landslide scars on the hillslope, (*e*) one of the mature forest catchments, (*f*) the channel of a middle-aged forest that was recently scoured by a debris flow, and (*g*) the channel in one of the mature forest catchments.
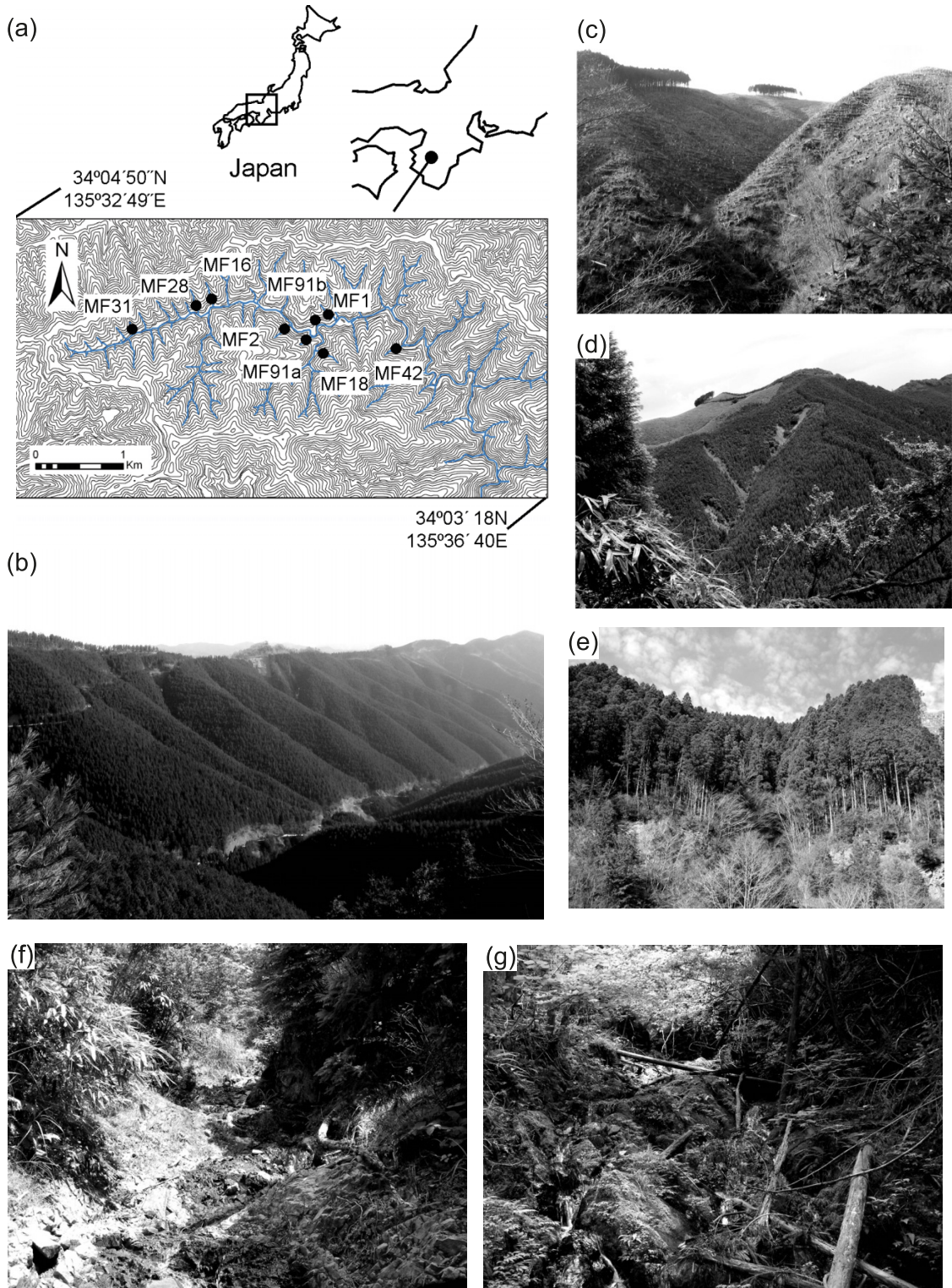
1967, 1971, 1976, 1984, 1989, 1994, 1998, and 2003. The photographs provided a range of possible years for the debris flow occurrences rather than the exact year of the occurrence (e.g., if a debris flow was first detected on photographs from 2003, the debris flow occurred sometime between 1998 and 2003). The most recent debris flows were detected in MF16

Table 1. Properties of the catchments and streams within the 50 m study reaches.

|	MF1	MF2	MF16	MF18	MF28	MF31	MF42	MF91a	MF91b	UF
Watershed area (ha)	4.7	6.6	6.2	5.9	6.5	3.8	9.0	5.1	2.5	7.7
Aspect	Southeast	Northeast	Southeast	Northwest	Southeast	Southeast	Northeast	Northeast	Southeast	Southeast
Year planted	2004	2003	1989	1987	1977	1974	1963	1914	1914	
Years of debris flow (years of aerial photographs with a new debris flow scar)	1948		1998	1994	1989	1984, 1989	1971		1948	
Mean channel slope (degrees)	20.6	22.5	25.6	21.4	21.6	24.5	27.6	27.8	26.1	23.0
Length of channel covered by logs/slash (m)	10.8	15.8	0	0	0	3.7	0	0	18.3	0
Proportion of bedrock in study reach	0.49	0.41	0.75	0.29	0.86	0.76	0.92	0.79	0.44	0.24
Mean flow width (m)	0.34	0.28	0.54	0.18	0.23	0.26	0.27	0.25	0.06	0.21

(1998) and MF18 (1994), with earlier debris flows in MF28 (1989), MF31 (1984 and 1989), and MF42 (1971) (Fig. 2). All of these debris flows appeared to occur at the same time as hillslope landslides and within 15 years after the last clearcutting, which is associated with root strength deterioration following clearcut harvesting (Imaizumi et al. 2008). Evidence of debris flows was detected in the oldest photograph (1948) in MF1 and MF91b, and no debris flows were detected in MF2, MF91a, and UF.

Each catchment has stream channels ranging in length from 300 to 500 m and in width from 1 to 5 m. All channels were typically incised and with exposed bedrock in at least their lower reaches, except in MF18 where sediment deposits covered the entire streambed for more than 150 m in the middle and lower sections. Upstream and middle sections of MF1, MF2, and MF91b were heavily covered by pieces of large wood recruited by past logging activities or windthrow. The riparian areas of the managed forest catchments were covered by deciduous trees and shrubs, dwarf bamboo, and herbaceous plants, even in recently logged forests. Field surveys were conducted in a 50 m reach within the lower section of each stream where flow was perennial. The mean gradients of the study reaches ranged from 20 to 28° (Table 1), which can be classified as scour zones of sediment according to Montgomery (1999). More than 50% of the study reach was exposed bedrock in MF16, MF28, MF31, MF42, and MF91a. In-channel sediments ranged from sand (<2 mm) to boulders (>256 mm) with D_{50} (the diameter for which 50% of the particles are smaller) ranging from 8 to 24 mm based on surveys in MF16, MF28, and MF31. Baseflow discharge in most of our study streams was approximately 1 L·s^{-1}, while in the stream of MF91b was less than 0.5 L·s^{-1} and in the streams of MF28 and MF42 was more than 1.5 L·s^{-1} based on field measurements of flow volume. In catchments where flow was continuously monitored (MF16, MF28, MF31, and MF 91b), discharge increased rapidly during heavy rainfall (Fig. 3 shows discharge data in MF16). Stream pH (range 7.5–7.7), electric conductivity (34.1–54.3 µS·cm^{-1}), and concentrations of Na$^+$ (3.5–4.0 mg·L^{-1}), K$^+$ (0.3–0.6 mg·L^{-1}), Ca^{2+} (3.1–5.5 mg·L^{-1}), Mg^{2+} (0.5–1.0 mg·L^{-1}), and Cl$^-$ (1.4–2.5 mg·L^{-1}) were similar among streams of managed forests. The stream of UF had a higher electric conductivity (110.6 µS·cm^{-1}) and higher concentrations of Ca^{2+} (14.1 mg·L^{-1}) and SO$_4^{2-}$ (7.2 mg·L^{-1}) than the streams of managed forests (range of SO$_4^{2-}$ 1.6–4.1 mg·L^{-1}).

In-channel abiotic characteristics

To evaluate potential solar radiation above stream channels, circular hemispherical photographs were taken at the upper, lower, and midpoints of the 50 m study reaches in March 2006 and June 2005 corresponding to periods before and after the emergence of deciduous leaves, respectively (photographs were not taken in MF91b in March 2006 due to clearcutting activities). The camera was mounted on a tripod 0.5 m above the stream surface in midchannel and leveled. Solar radiation was determined using Gap Light Analyzer image analysis software (Frazer et al. 1999) based on canopy openness (percent sky in the hemisphere), catchment aspect, channel slope gradient, latitude, and elevation of each stream.

Fig. 2. Relationship between forest age and debris flow history in the 10 streams studied. Debris flow history was determined using aerial photographs, which were available for the years indicated on the *y*-axis (the number of years prior to 2005 in parentheses). Debris flows occurred in the time intervals between consecutive aerial photographs rather than in the years that the photographs were taken.
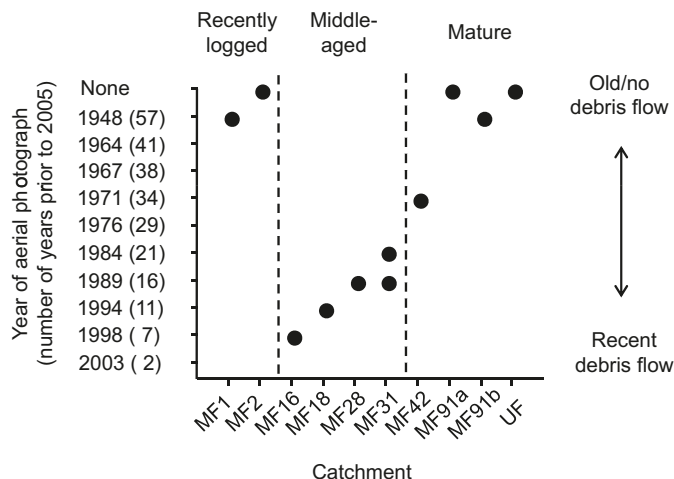
Stream water temperature was recorded from December 2004 to March 2006 using submersible temperature loggers with an accuracy of ±0.2 °C (StowAway Tidbit Data Loggers; Onset Computer Application, Bourne, Massachusetts). The loggers were housed in polyvinyl chloride (PVC) pipes and placed on the streambed in the downstream portion of study reaches with at least 0.2 m water depth. Temperature was recorded every 10 min. Although the recording period was not exactly the same in all streams, all loggers recorded consistently from April to November 2005.

Stream water was sampled 10 times at intervals of 15–75 days throughout the study period (Fig. 3). Stream water was filtered through a 0.47 µm pore size glass fiber filter to determine concentrations of dissolved organic carbon (DOC) and NO_3^-. DOC was measured using a total organic carbon analyzer (Shimadzu TOC-V) and NO_3^- was determined by ion chromatography (Dionex ICS-90).

All pieces of wood in two size-classes (large woody pieces: diameter >0.1 m, fine woody pieces: diameter 0.03–0.1 m) were counted in the study reaches in June 2005. Litter accumulations (leaves, needles, and branches) were also estimated in June and November 2005 by recording streambed coverage (square metres) of all litter accumulations greater than 0.0025 m².

Principal components analysis was performed to demonstrate correlations among abiotic variables and overall abiotic characteristics of the 10 streams. For this analysis, we used mean solar radiation (June), means and ranges of water temperatures (from April to November), mean concentrations of NO_3^- and DOC, abundances of all woody pieces, and litter accumulations (June). Variables except temperatures were log transformed prior to the analysis.

Macroinvertebrate communities

It was not practical to quantitatively collect macroinvertebrates from the streambeds over multiple periods within a year because narrow channels and high bed roughness rela-

tive to water depth (i.e., bed roughness usually exceeded water depth) limit the use of typical samplers (e.g., Surber net) at multiple positions. Therefore, we compared the macroinvertebrates collected by anchored drift nets 10 times throughout the year (December 2, December 17, March 2, April 22, May 23, June 24, July 29, August 23, September 27, and November 7) (Fig. 3) among all streams. Because drift nets collect many individuals moving either passively or actively downstream, we assumed that the community structure of benthic invertebrates is partially reflected in drift samples. To examine this assumption, we also collected macroinvertebrates from the streambeds on a single occasion for each stream and compared these with macroinvertebrates in drift samples.

To collect macroinvertebrates by drift nets (0.25 mm mesh, 1 m length), the flow on exposed bedrock was diverted using sandbags into a 10 cm diameter PVC pipe (length 50 cm) at the downstream end of each study reach (Piccolo and Wipfli 2002). We molded putty into the gaps between bedrock and the pipe to capture more than 75% of the total discharge. The net was attached to the downstream end of the pipe with a rubber band and macroinvertebrates were collected continuously for 24 h; this covers diel movement patterns of invertebrates (i.e., strong peaks at dawn and dusk). Once during this 24 h period, we measured the volume of flow passing through the pipe using a graduated cylinder to estimate the flow rate passing through the net.

Benthic macroinvertebrates were collected from both sediment- and bedrock-dominated substrates with a modified kick sampler in June 2005. A PVC pipe was placed 30–50 cm downstream of the sampling position and the flow was diverted into the pipe using the same methods as used with drift samples. Materials within an area of approximately 900 cm² on the streambed were flushed by hand and running water after placing a 0.25 mm mesh net at the end of the pipe. For each substrate type, we collected from three positions and the samples were combined into one (i.e., one sample for each substrate in each stream).

All invertebrate samples were fixed in 10% formalin immediately after collection. In the laboratory, each sample was washed through a 1 mm mesh sieve and aquatic invertebrates on the sieves (i.e., macroinvertebrates) were sorted from other organic materials. Macroinvertebrates were identified to the lowest taxonomic level possible (usually genus or species) and counted. Dry mass was also estimated by measuring individual body length (to the nearest millimetre) and then applying known length–mass relationships (Benke et al. 1999). Taxa without known relationships (e.g., noninsect taxa) were directly weighed after drying at 60 °C for 48 h. Formalin-preserved animals are assumed to have weights that are very close to those of fresh animals (Benke et al. 1999).

Macroinvertebrates were classified into different groups according to three schemes: (*i*) functional feeding groups, (*ii*) life-form types, and (*iii*) longitudinal distribution groups. In the classification of functional feeding groups, grazers, shredders, collectors, filterers, and predators were identified (Cummins 1973). In the classification of life-form types, clingers, swimmers, crawlers, burrowers, divers, and skaters were identified (modified from "mode of existence" in Merritt and Cummins 1996). Each life-form type corresponds to certain habitat conditions, and life-form classification can

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Fig. 3. Daily flow discharge for the stream of MF16 during the study period. Arrows indicate the timing of collections of water samples and invertebrates by drift net.
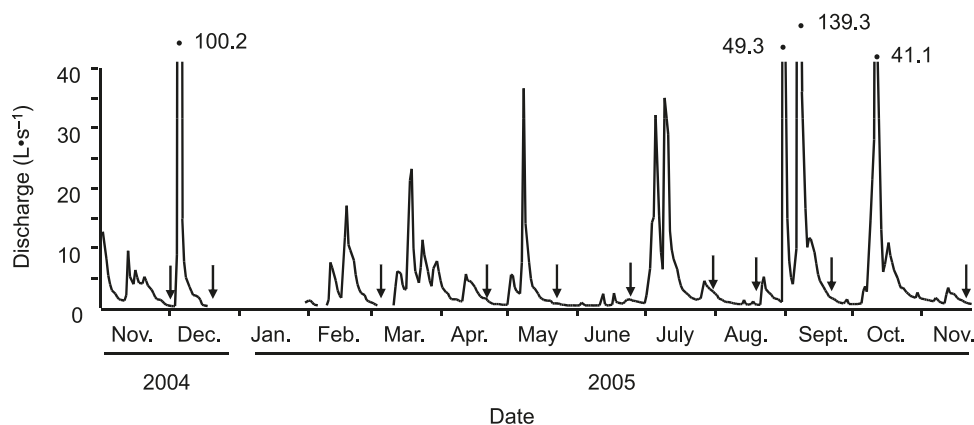
provide information on the hydraulic features of streams. For instance, the habitats of clingers are associated with stony substrates that are typical of fast-current conditions, whereas habitats of crawlers are associated with organic or sandy substrates that are typical of slow-current conditions. Longitudinal distribution groups were indentified to examine responses of macroinvertebrates according to the reliance and dominance in headwater habitat. According to known longitudinal distributions, macroinvertebrates were classified into headwater taxa (mainly occurring in first-order channels or seeps), small-stream taxa (second- or third-order channels), and larger-stream taxa (higher than third-order channels). Functional feeding group and life-form types were assigned according to Kagaya (1990), Merritt and Cummins (1996), and Takemon (2005), and longitudinal distribution groups were assigned according to Uchida (1987), Kagaya et al. (1998), and Kawai and Tanida (2005). Taxa with limited information for classification were assigned based on other species in the same genus or family (the longitudinal group of a few taxa could not be specified due to high variations within the genus or family). Corresponding groups for each taxon are listed for taxa used in analysis in Appendix A.

The number (or dry mass) of macroinvertebrates captured per 24 h was used to express abundance, and flow rate was considered as one of the physical variables that may affect abundance. The abundance of invertebrates collected by drift nets is often standardized by the flow volume passing through the net (Statzner et al. 1987; Allan 1995), although the relationships between flow volume and invertebrate abundance are variable (Statzner et al. 1987; Winterbottom et al. 1997). In addition, flow passing through the net was shallow (<2–3 cm depth), and many individuals possibly enter the nets through walking on the bed as well as via the water column. Thus, the number (or dry mass) of macroinvertebrates captured per 24 h was calculated during each period. In addition, mean number (or dry mass) of winter, spring, summer, autumn, and all sampling periods was calculated by averaging the values of corresponding periods (winter: December 2 and 17, spring: March 2, April 22, and May 23, summer: June 24, July 29, and August 23, autumn: September 27 and November 7). For benthic samples, the density of macroinvertebrates was calculated (i.e., number of individuals or dry mass per 1 m² of streambed). Since we collected benthic samples during a single period, all

streams had single values for sediment and bedrock macroinvertebrate densities.

For both drift and benthic samples, detrended correspondence analysis (DCA) ordination was used to quantify major variations in community structure among the 10 streams and to determine which groups of taxa are relevant to the variations based on the abundance data of 40 dominant taxa. DCA was conducted using PC-ORD version 5 (MjM Software, Gleneden Beach, Oregon). Abundance data were log transformed prior to these analyses. The among-stream abundance pattern of different groups (e.g., shredders and grazers) was also examined by calculating an averaged standardized abundance for each group. In the calculation, abundance of each taxon was standardized by the maximum abundance of the taxon among the streams, and the standardized abundance was averaged for each invertebrate group.

Statistical tests

To test for differences in abiotic and invertebrate variables among the 10 streams, a two-way ANOVA without replications was performed using stream ($n = 10$) and sampling time ($n = 10$) as factors. This test was conducted for those variables with 10 sampling occasions, including concentrations of NO_3^- and DOC and number or mass of macroinvertebrates in drift samples (total macroinvertebrates, dominant taxa, and functional feeding groups). For solar radiation, two-way ANOVA with replications ($n = 3$) was conducted using stream ($n = 10$) and period (June and March) as factors (stream MF91b was omitted due to no March data). For ANOVAs with significant stream effects, multiple mean comparisons were made using Tukey's test. Data were log transformed or ranked to normalize distributions and standardize variance structures prior to statistical analysis. These analyses were performed using SPSS version 15 (SPSS Inc., Chicago, Illinois). For all tests, an α value of 0.05 was used for statistical significance.

Results

In-channel abiotic characteristics

Solar radiation input was significantly lower in June than in March (ANOVA: df = 1, $F = 24.893$, $p < 0.001$) due to leaf emergence of the deciduous riparian trees (Fig. 4). Solar radiation was two to four times higher in streams of MF1,

MF2, and MF16 than in streams of older forests and the difference was significant (Tukey's test: $p < 0.05$) (Fig. 4). Solar radiation was also significantly higher in the stream of MF18 than in streams of MF42 and MF91a. Differences in solar radiation between June and March varied significantly among streams (ANOVA: stream × period interaction, df = 8, $F = 2.417$, $p < 0.034$).

Seasonal changes in stream temperatures were evident in all streams according to the mean and range of temperatures in four consecutive periods (April–May, June–July, August–September, and October–November) (Fig. 4). Differences in mean temperature among the 10 streams were relatively smaller in April–May (range 10.2–12.4 °C) and October–November (10.8–12.9 °C) compared with June–July (12.7–16.0 °C) and August–September (13.7–17.2 °C). In all periods, mean temperature was the highest in the stream of UF and was the lowest in streams of MF18 and MF91b (Fig. 4). The range of temperature was always the largest in the stream of MF16 and the smallest in streams of MF18 and MF91b. The range of temperature was also smaller in streams of mature forests (MF42, MF91a, MF91b, and UF) compared with other streams (except MF18).

Concentrations of NO_3^- in the streams of recently logged forests were two to eight times higher during most collection periods compared with the other streams (Tukey's test: $p < 0.05$) (Fig. 4). In the stream of MF91b, NO_3^- concentrations fluctuated from 0.7 mg·L^{-1} in winter to 5.1 mg·L^{-1} after clearcutting in June, approximately the same range as in the streams of recently logged forests. Concentrations of DOC were also significantly higher in the stream of MF2 compared with streams of MF18, MF28, MF31, MF42, and MF91a (Tukey's test: $p < 0.05$).

Streams of MF1, MF2, MF91b, and UF had more than 10 pieces of small woody debris (diameter 3–10 cm) per 50 m of stream reach, while streams of middle-aged forests had lesser amounts of both small and large woody debris (Fig. 4). Streams of MF28 and younger forests had consistently lower litter accumulations within their channels in June compared with older forest streams. Litter accumulations increased in November when leaves were abundant after leaf abscission, especially in streams of MF16, MF28, and MF42 (Fig. 4).

In the principal components analysis of seven abiotic variables, the first and second axes accounted for 73.0% of the total variance of abiotic variables among the 10 streams (Fig. 5). Streams of recently logged forests (MF1 and MF2) were characterized by high concentrations of DOC and solar radiation. Streams of MF16 and MF28 were segregated from other streams along the second axis, which was positively correlated with temperature range and negatively correlated with litter accumulation. Streams of middle-aged forests (MF16, MF18, MF28, and MF31) were characterized by lower amounts of woody debris and lower NO_3^- concentrations. Streams of MF91a, MF91b, and UF were characterized by greater litter accumulations and lower temperature ranges.

Macroinvertebrate community

Total abundance and dominant taxa

The mean flow rate passing through drift nets ranged from 0.32 to 1.64 L·s^{-1} among the 10 streams (Table 2);

Fig. 4. Solar radiation incident above the channel, stream temperature (mean, maximum, and minimum) of four periods, mean concentrations of NO_3^- and DOC, abundance of woody debris, and litter accumulations in the channel. Error bars indicate ±1 SD. For MF91b, no data were obtained for solar radiation in March 2006 and for litter accumulation in November 2005. Different superscripts denote a significant difference (Tukey's test: $p < 0.05$) in values among streams.
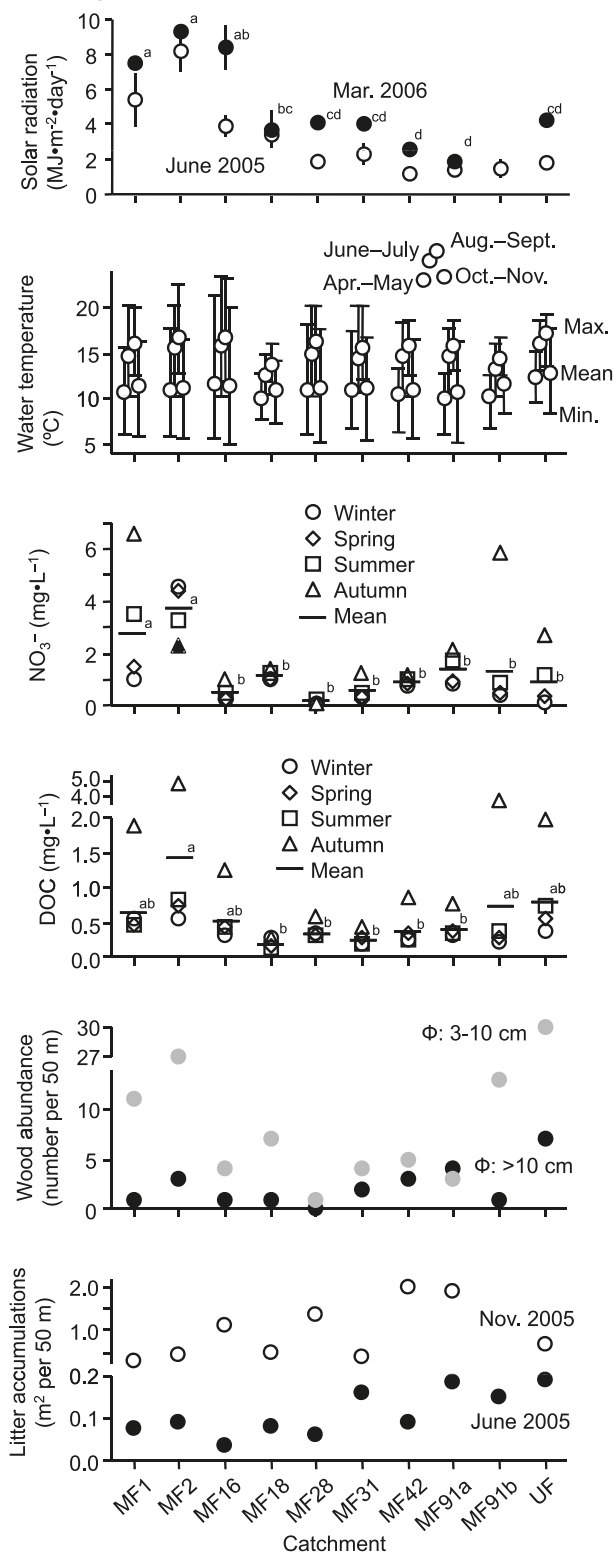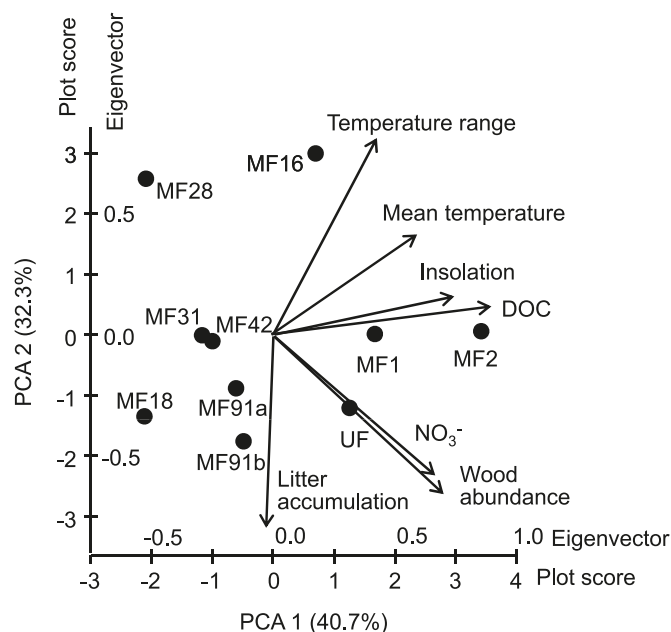
Fig. 5. Results of principal components analysis based on seven stream abiotic characteristics.

Fig. 6. Mean number and dry mass of total macroinvertebrates collected by drift net per 24 h in winter, spring, summer, autumn, and the entire period.

greater discharges were associated with larger watershed areas (e.g., MF28 and MF42) (Table 1). While no strong seasonal patterns were evident in the total number of macroinvertebrates in drift collections, many streams had lower abundance in autumn (in seven of the 10 streams) and winter (Fig. 6). Life cycles and activities of invertebrates related to stream temperature surely affected the temporal variation in abundance. In addition, there was some evidence of reductions in abundance after the highest peak flows (early December and early September) (Fig. 3). The total number of invertebrates was significantly higher in the stream of MF2 than in streams of MF18, MF31, MF91a, and MF91b and also significantly higher in streams of MF16 and UF than in the stream of MF31 (Table 2). Overall, a total of 91 taxa were captured in the drift samples, but fewer than 10 individuals were collected for more than half of these taxa throughout the study period. The most dominant taxon in streams of mature forests (MF42, MF91a, MF91b, and UF) and MF2 was *Gammarus nipponensis*, whereas the dominant taxon in the other streams was *Baetis thermicus* (Table 2). The abundance (including the presence or absence) of some taxa differed significantly among streams (Table 2). For instance, *G. nipponensis* was completely absent in all streams of middle-aged forests (MF16, MF18, MF28, and MF31). Abundance of *B. thermicus* was significantly higher in the stream of MF16 than in the stream of MF91b, and abundance of *Baetis* sp. (sp. F in the Japanese identification) was significantly higher in MF16 and MF28 than in streams of all recently logged forests and mature forests (Table 2).

Some taxa that were dominant in drift samples, including *G. nipponensis* and *B. thermicus*, were also dominant in benthic samples, either in sediment or in bedrock substrate (Table 3). The density of total macroinvertebrates was substantially higher for sediment than from bedrock in most streams. For sediment, the most dominant taxon was *G. nipponensis* in streams of recently logged and mature forests,
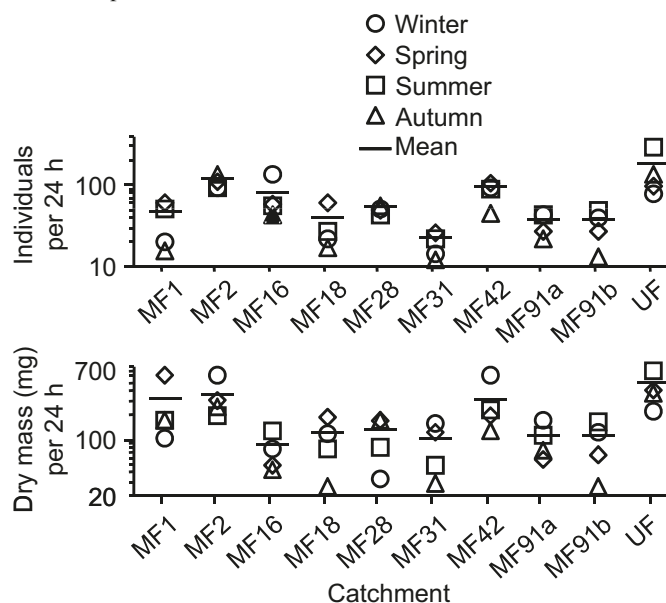
whereas *Togoperla limbata* or *Eubrianax* sp. was the most dominant in streams of middle-aged forests. On bedrock, the most dominant taxon was *B. thermicus* in the streams of MF1, MF16, MF28, and MF31 and *Yoraperla uenoi* in the streams of MF2, MF18, and MF42. *Gammarus nipponensis* was completely absent in both sediment and bedrock in streams of middle-aged forests. The density of *Baetis* sp. on sediment was higher in streams of middle-aged forests than in the other streams.

Among-stream community variations and invertebrate groups

In DCA ordination for drift samples (Figs. 7 and 8*a*), the proportion of the entire variance in macroinvertebrate communities explained by the first and second axes was 23%–70% for each season and 71% for the entire period. In each season and for the entire period, the communities of middle-aged forests (lower first-axis scores) were separated from the communities of recently logged and mature forests (higher first-axis scores). A similar separation among streams was observed for DCA ordination for benthic samples (not shown in the figures).

In the DCA plots of the entire period, shredders typically had lower first-axis scores than grazers and filterers (Fig. 8*b*, left panel), crawlers typically had lower first-axis scores than swimmers and clingers (Fig. 8*c*, left panel), and headwater taxa and small-stream taxa typically had lower first-axis scores than larger-stream taxa (Fig. 8*d*, left panel). Differences in the standardize abundance of invertebrate groups between streams of middle-aged forests and the other streams were tested by one-way ANOVA (Table 4). The standardized abundances of shredders, crawlers, and headwater taxa were significantly lower in streams of middle-aged forests than the other streams, while standardized abundances of grazer, swimmer, and larger-stream taxa were significantly higher in streams of middle-aged forests (Figs. 8*b*–8*d*, right panels; Table 4).

Table 2. Flow discharge through drift nets and mean macroinvertebrate abundance and weight collected by the drift net in each stream over ten sampling occasions from December 2004 to November 2005.

	MF1	MF2	MF16	MF18	MF28	MF31	MF42	MF91a	MF91b	UF	F	p
Flow discharge (L·s⁻¹)												
Mean	1.00	0.74	0.96	1.00	1.64	0.68	1.44	1.10	0.32	1.08		
SD	0.48	0.30	0.26	0.26	0.35	0.25	0.36	0.25	0.24	0.53		
Macroinvertebrate abundance (individuals per 24 h)												
Geothelphusa dehaani	0.3	1.4	0.8	0.6	0.7	1.3	3.8	0.5	0.4	0.6	0.82	0.603
Gammarus nipponensis	4.9d	89.5a	0e	0e	0e	0e	36.3abc	14.3cd	21.2bcd	161.1ab	40.79	<0.001
Baetis thermicus	13.4ab	7.7ab	40.5a	17.4ab	25.7ab	8.3ab	20.9ab	9.1ab	6.0b	6.5ab	2.66	0.009
Baetis sp.	0b	0.1b	3.7a	0.4ab	3.1a	0.6ab	0.3b	0b	0.2b	0b	10.38	<0.001
Epeorus spp.	1.3	0.9	3.4	0.9	3.4	1.4	1.3	2.9	1.4	1.0	2.12	0.04
Yoraperla uenoa	0.5bc	3.1a	0.6c	3.6ab	0.5c	0.6abc	2.7a	1.3abc	0c	0c	7.91	<0.001
Togoperla limbata	2.8ab	0.6ab	1.0ab	2.7a	1.8ab	0.6ab	0.6ab	0.1b	0.4ab	1.1ab	2.30	0.023
Uenoa tokunagai	0.5abc	3.4a	1.9abc	0.4abc	2.6abc	0.1bc	2.3ab	0.2bc	0.1bc	0c	5.12	<0.001
Hydrocassis lacustris	1.9ab	2.8a	1.1ab	1.0ab	1.3ab	0.1b	1.1ab	1.6ab	0.3b	1.2ab	3.11	0.003
Simulium spp.	1.3b	0.3b	10.6a	0.7b	1.2b	0b	2.8b	2.2b	0.1b	0.2b	7.74	<0.001
Total	46.3abc	121.0a	80.0ab	39.1bc	54.9abc	22.3c	87.4ab	38.7bc	37.6bc	181.6ab	5.11	<0.001
Macroinvertebrate mass (mg dry mass per 24 h)												
Shredders	18.3b	224.4a	0.3c	0.4c	0.1c	1.2c	128.8a	55.3ab	76.7ab	387.8a	49.55	<0.001
Grazers	10.9abc	19.3abc	33.4a	15.7abc	18.5ab	8.4abc	29.4abc	9.7abc	7.1bc	7.6c	3.91	<0.001
Collectors	3.4	11.8	1.4	8.7	1.2	0.8	1.1	0	2.1	1.0	2.09	0.04
Filterers	1.0ab	1.8ab	2.0ab	0.6ab	1.7ab	0b	8.3ab	6.9a	0.3ab	1.1ab	2.95	0.004
Predators	291.4a	100.8ab	47.8ab	95.6ab	108.6ab	90.4ab	101.3ab	38.6ab	25.7b	103.2ab	2.93	0.005
Total	325.0ab	358.1a	84.9b	121.0ab	130.2ab	100.7b	268.9a	110.6ab	111.8ab	500.6a	4.25	<0.001

Note: Results of two-way ANOVA (effect of stream on abundance and mass) are also shown. Different letters denote a significant difference (Tukey's test: $p < 0.05$) among streams.

Table 3. Macroinvertebrate abundance and mass in sediment and bedrock benthic samples from each stream.

	MF1	MF2	MF16	MF18	MF28	MF31	MF42	MF91a	MF91b	UF
Macroinvertebrate abundance (number per m^2 of streambed)										
Sediment										
Geothelphusa dehaani	41	41	52	44	63	7	122	11	0	56
Gammarus nipponensis	552	1633	0	0	0	0	1059	1230	1863	2593
Paraleptophlebia sp.	111	0	152	44	70	56	7	41	0	15
Baetis sp.	15	0	163	41	156	215	22	0	0	0
Epeorus spp.	7	26	48	126	274	204	63	4	11	15
Togoperla limbata	107	100	300	170	322	137	226	89	52	133
Amphinemura spp.	15	4	11	26	22	56	11	204	44	7
Nemoura spp.	33	26	19	133	11	270	959	926	119	44
Dolophilodes spp.	78	11	4	26	48	19	163	33	89	215
Eubrianax sp.	63	85	89	33	37	348	7	7	7	26
Total	1907	2219	1481	1081	1656	1985	3341	3030	2496	3478
Bedrock										
Gammarus nipponensis	15	78	0	0	0	0	4	0	15	122
Ephemerella setigera	59	22	22	11	33	59	4	19	0	0
Baetis thermicus	337	7	270	193	89	404	22	85	0	100
Epeorus spp.	52	11	141	4	48	67	19	15	4	33
Yoraperla uenoi	81	137	96	211	4	56	226	115	0	0
Indonemoura spp.	100	37	41	4	7	52	15	137	15	0
Micrasema hanasensis	19	15	193	30	11	7	19	15	0	0
Micrasema sp.	0	115	67	4	0	4	0	0	4	0
Grouvellinus nitidus	33	19	37	4	7	119	0	44	15	11
Simulium spp.	37	0	70	0	48	0	4	11	0	0
Total	848	493	1089	481	289	796	348	533	52	344
Macroinvertebrate mass (mg dry mass per m^2 of streambed)										
Sediment										
Shredders	531	514	3	9	3	19	559	892	1202	1020
Grazers	33	52	48	31	45	91	37	46	13	89
Collectors	78	12	31	10	51	55	19	53	1	5
Filterers	62	4	2	15	110	58	127	277	36	31
Predators	1358	347	2272	1133	1031	874	1630	774	441	657
Total	2062	928	2455	1199	1240	1097	2372	2041	1694	1801
Bedrock										
Shredders	20	53	3	0	1	1	5	4	9	33
Grazers	120	84	161	54	43	78	46	58	3	42
Collectors	21	3	34	2	25	8	6	1	0	0
Filterers	1	40	3	0	3	0	0	1	0	1
Predators	3	8	28	19	1	6	1	0	0	0
Total	165	188	230	76	73	93	59	65	12	76

Note: Samples were combined from three different positions in each channel in June 2005.

Mass of functional feeding groups

Mass of total macroinvertebrates collected by drift nets varied temporally (Fig. 6). Similar to the seasonal trends in abundance of individuals, the mass of total macroinvertebrates in drift samples was lower during autumn in many streams (Fig. 6). Mass of total macroinvertebrates was significantly higher in streams of MF2, MF42, and UF than in streams of MF16 and MF31 (Table 2; Fig. 6). Mass of shredders was two to three orders of magnitude higher in streams of recently logged forests and mature forests (mean 18–388 mg) than in streams of middle-aged forests (0.1–1.2 mg), and the difference was significant (Tukey's test: $p < 0.05$) (Table 2). Mass of shredders was also significantly higher in streams of MF2, MF42, and UF than in the stream of MF1. Mass of grazers was significantly higher in the stream of MF16 (33 mg) than in streams of MF91a and UF (7–8 mg) and also significantly higher in the stream of MF28 (19 mg) than in the stream of UF. In streams of recently logged and mature forests, shredders contributed 54%–98% of the nonpredator dry mass and *G. nipponensis* contributed >90% of the shredder dry mass. In streams of middle-aged forests, grazers comprised 61%–91% of the nonpredator dry mass. Collectors and filterers contributed <10% of the nonpredator dry mass in most streams. Mass of predators was significantly higher in the stream of MF2 than in the stream of MF91b.

We observed similar differences in the dry masses of functional feeding groups in benthic samples (Table 3). Mass of shredders, predators, and total macroinvertebrates was substantially higher in sediment than in bedrock sam-

Fig. 7. Detrended correspondence analysis ordination for macroinvertebrate communities based on the abundance of 40 dominant taxa in drift samples for winter, spring, summer, and autumn periods.
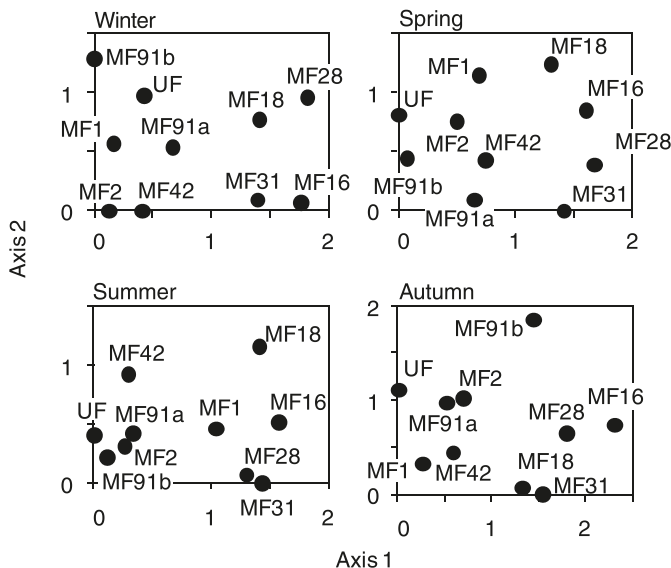
ples in all of the streams. Shredders dry mass in sediment samples was two to three orders of magnitude higher in streams of recently logged and mature forests (514–1212 mg·m^{-2}) than in streams of middle-aged forests (3–19 mg·m^{-2}). In sediment samples, shredders contributed 70%–96% of the nonpredator dry mass in the streams of recently logged and mature forests, while grazers, collectors, and filterers contributed 85%–99% of the nonpredator mass in streams of middle-aged forests.

Discussion

In this study, we evaluated abiotic characteristics and macroinvertebrate communities of 10 steep headwater streams with different legacies of forest clearcutting and debris flow occurrence. Although among-stream patterns in many of the abiotic variables were largely associated with legacies of forest clearcutting, the major variances in macroinvertebrate communities among the 10 streams were associated with legacies of debris flow occurrence. Herein, we discuss (*i*) effects of forest clearcutting and debris flows on the abiotic stream environment, (*ii*) effects of forest clearcutting and debris flows on the macroinvertebrate community, (*iii*) mechanisms of debris flow influences on the macroinvertebrate community, and (*iv*) effects of debris flow on food web structures in headwater streams.

Responses of in-channel abiotic characteristics to clearcutting and debris flows

Abiotic characteristics of headwater streams such as solar radiation input and nutrient concentrations appear to be largely affected by forest clearcutting. High concentrations of NO$_3^-$ in streams of recently logged forests are likely associated with rapid mineralization and leaching from hillslopes after clearcutting, as reported for many small catchments in North America (e.g., Bormann and Likens 1979; Gundersen et al. 2006). Due to high light availability and high nutrient levels, the potential for primary production would be high in

these streams. Greater solar radiation input also likely increased the variation in water temperatures in these streams as compared with streams of mature forests. However, the variation in water temperatures in streams of recently logged forests was similar to that in streams of MF28 and MF31 with lower solar radiation inputs. The slash that covered portions of the channels of recently logged forests (22%–32%) as well as the channel incision might have mitigated the temperature increase of stream water (Jackson et al. 2001).

Although responses of abiotic characteristics to debris flows were not as clear as the responses to clearcutting, some patterns in abiotic variables appear to be associated with the occurrence of debris flows. Woody debris is supplied to the channel by clearcutting and thinning of conifers and by windthrow and fall down of riparian trees and can potentially accumulate in the channel for more than 30 years (Gomi et al. 2001; Gurnell et al. 2002). Thus, the depletion of wood in streams of middle-aged forests (MF16, MF18, MF28, and MF31) is likely due to debris flows that occurred within a period of 7–21 years after harvesting. Debris flows can also remove growing riparian vegetation and undercut stream banks and thus weaken support for riparian trees and extend the recovery period for riparian canopies. Despite low canopy openness in streams of MF28 and MF31, trees did not fully cover the channels, thus allowing midday radiation. Thus, it may take at least 30 years for full canopy closure after clearcutting, which is relatively long compared with other studies reporting closure within 15 years (Beschta et al. 1987; Johnson and Jones 2000).

Valley and channel characteristics would have influenced some of the patterns in abiotic characteristics associated with clearcutting and debris flow occurrence. For instance, canopy openness and solar radiation were greater in the stream of MF2 than in the stream of MF1, which appears to be related to a difference in steepness of the valley incision between these streams. In addition, smaller temperature variations in the stream of MF18 compared with the stream of MF16 are potentially associated with greater sediment cover in the channel of MF18, which can promote heat exchange in hyporheic zones (Moore et al. 2005*b*). Finally, steeper channel slopes and lower sediment coverage in streams of MF42 and MF91a may reduce the potential for accumulation of woody debris as compared with streams of MF91b and UF. These local variations in valley and channel characteristics can be sources of variation in macroinvertebrate communities among streams with similar forest ages in the discussion that follows.

Responses of macroinvertebrate community to clearcutting and debris flows

In this study, macroinvertebrates in drift and benthic samples showed many consistencies in among-stream patterns of community structure. The dominant taxa in drift samples, including *G. nipponensis* and *B. thermicus*, were also dominant in benthic samples, either from sediment or from bedrock. Consistencies in among-stream patterns between drift and benthic samples include the absence or presence of *G. nipponensis*, the abundance of *Baetis* sp., major variations in community composition as shown by DCA ordination, and shredder dry mass. Based on these consistencies, we can

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Fig. 8. (*a*) Detrended correspondence analysis ordination for macroinvertebrate communities based on the abundance of 40 dominant taxa in drift samples of the entire period. (*b*–*d*) Detrended correspondence analysis plots of the 40 taxa (left panels) and mean standardized abundance of each invertebrate group (right panels) are also shown. Taxa were classified according to (*b*) functional feeding group, (*c*) life-form type, and (*d*) longitudinal distribution group. The number of taxa in each group used in the analyses is shown in parentheses.
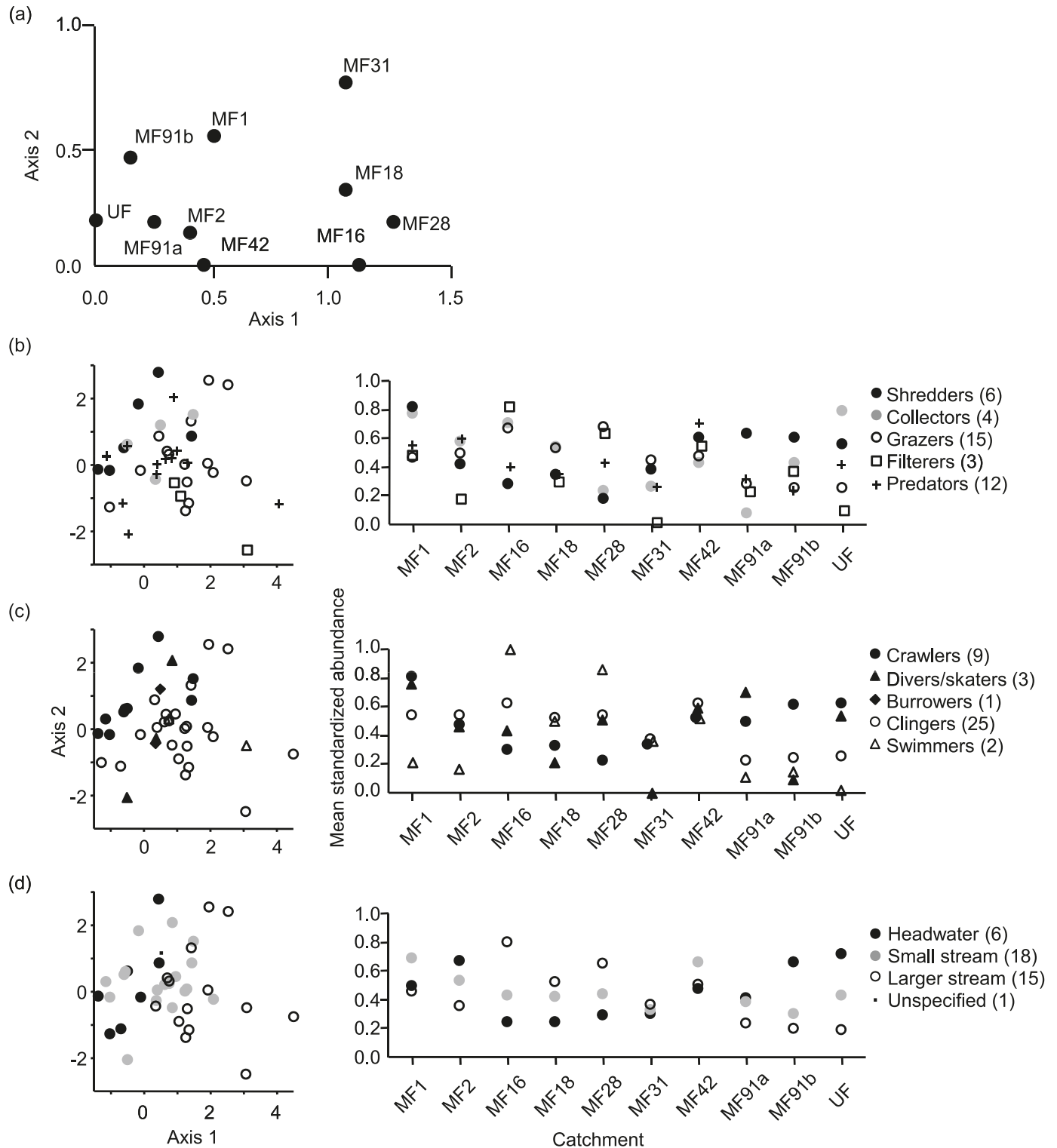
conclude that among-stream patterns of benthic macroinvertebrate communities were largely reflected in drift samples.

There were no remarkable changes in the macroinvertebrate communities due to clearcutting, except in a few grazer taxa, despite the changes in abiotic condition (e.g., solar radiation and nutrients). Many previous studies have shown marked changes of macroinvertebrate communities after clearcutting in headwaters of the Appalachian Moun-

Table 4. Mean standardized abundance of each invertebrate group collected by drift nets in the streams of recently logged forests and mature forests ($n = 6$) and the streams of middle-aged forests ($n = 4$) and results of one-way ANOVA that tests the difference between two groups of streams.

	Streams of recently logged forests and mature forests	Streams of middle-aged forests	F	p
Functional feeding group				
Shredders	0.60	0.29	17.016	0.003
Grazers	0.37	0.58	7.878	0.023
Collectors	0.51	0.43	0.239	0.638
Filterers	0.32	0.44	0.506	0.497
Predators	0.47	0.36	1.17	0.311
Life-form type				
Clingers	0.40	0.51	1.157	0.313
Swimmers	0.20	0.68	10.997	0.011
Crawlers	0.56	0.30	19.76	0.002
Burrowers	0.52	0.40	0.168	0.693
Diver and skaters	0.52	0.29	2.428	0.158
Longitudinal distribution group				
Headwater taxa	0.57	0.27	20.811	0.002
Small-stream taxa	0.49	0.40	1.357	0.278
Larger-stream taxa	0.32	0.58	6.663	0.033

tains and the Oregon Coast Ranges (Newbold et al. 1980; Webster et al. 1983; Stone and Wallace 1998); grazers usually increased, while shredders decreased in the year of clearcutting. Other studies have shown variable responses of grazers and shredders after clearcutting. Danehy et al. (2007) and Moldenke and Ver Linden (2007) noted only small responses of grazers after clearcutting due to the dominance of periphyton, which is resistant to grazing. Haggerty et al. (2004) and Hernandez et al. (2005) observed increases of shredders due to changes in availability of nutrient-rich leaves. The effects of clearcutting in our study might be mitigated by steep hillslopes and channel incision that limit radiation inputs and by riparian shrubs that continuously supply litter after clearcutting. At a smaller scale, the effects of clearcutting might be mitigated by the presence of slash cover over streams, which maintains shade and provides an input of detritus, although slash covered only a portion of our study reaches. In addition, we did not observe fine-sediment loading and deposition in streams of recently logged forests partly due to limited soil disturbances during clearcutting associated with the skyline harvesting methods and the absence of nearby contributing logging roads.

The major variations in macroinvertebrate communities among the 10 streams were largely associated with the legacies of debris flow occurrence. Streams of middle-aged forests, which experienced debris flows within the previous 7–21 years, had macroinvertebrate communities different from those of recently logged and mature forests, which did not experience debris flows for more than 34 years. The difference was most pronounced for an amphipod, *G. nipponensis*, which was dominant in streams of recently logged and mature forests but completely absent in streams of middle-aged forests. Macroinvertebrate communities were distinctly separated between these two stream groups in DCA ordinations, which were associated with the differences in composition of functional feeding groups, life-form types, and longitudi-

nal distribution groups. These findings indicate that the occurrence of debris flows is the factor causing the major variation in macroinvertebrate community structure among these headwater streams.

Although the major variation in macroinvertebrate communities among headwater streams was associated with the legacies of debris flow occurrence, community variations that cannot be explained by the legacies were also evident. Variations in watershed area, aspect, and valley and channel morphology among the headwater streams can be sources of variability in macroinvertebrate communities (Naiman and Bilby 1998; Richardson et al. 2005; Clarke et al. 2008). Areas of sediment cover and exposed bedrock within a stream reach are also sources of variation in macroinvertebrate communities among headwater streams because assemblage structure largely differed between these substrates. The differences in community structure between these substrates were explained by lower abundances of shredders, collectors, filterers, and predators in bedrock, while some grazer taxa had higher abundance in bedrock. In addition to physical habitat heterogeneity among headwater streams, Clarke et al. (2008) noted that high variations in macroinvertebrate communities were associated with limited dispersals and turnover of macroinvertebrates among headwater streams; this concept may also apply to our streams.

Mechanisms of debris flow influences on invertebrate communities

Debris flows likely affected invertebrate communities by altering the hydraulic conditions in the channel and associated habitats for invertebrates. The life-form types that were abundant in streams with recent debris flows were swimmers and clingers, which are typically associated with fast-flow habitats, whereas crawlers, which are typically associated with slow-flow habitats, were abundant in streams with old or no debris flows. This community pattern implies

that slow-flow conditions decreased and fast-flow conditions increased in the stream channels after debris flows. Although we did not emphasize habitat variables in this study, the depleted amounts of wood debris in streams of middle-aged forests support this idea. Woody debris is important for creating depositional environments in headwater streams (Bilby 1981; Wallace et al. 1995; Gurnell et al. 2002) and shifts in invertebrate communities from lotic to lentic taxa have been observed after an addition of woody pieces (Wallace et al. 1995). Thus, debris flows likely affected macroinvertebrate communities through modifying the hydraulic environment (i.e., a decrease of lentic habitat and an increase of lotic habitat) by removing pieces of wood in the channel and destroying in-channel structures (MacFarlane and Wohl 2003).

Changes in type and availability of food may also have affected invertebrate communities. Both ordination and comparisons of standardized abundance showed that shredder taxa, which usually feed on plant litter, were less abundant in streams of middle-aged forests. The availability of litter may be limited in streams of middle-aged forests due to low retentiveness of organic matter in the channels. Woody debris, which was depleted in streams of middle-aged forests, plays an important role in the retention of organic matter (Bilby 1981; Raikow et al. 1995; Brookshire and Dwire 2003). Smaller litter accumulations in June (despite high amounts in November after leaf fall) in streams of MF16 and MF28 suggest a low retentiveness for organic matter in these streams.

Another possible mechanism by which debris flows influence macroinvertebrate communities relates to the ability of invertebrates to disperse and colonize (in contrast with the environmental changes already discussed). During the occurrence of debris flows, invertebrates appeared to be killed or removed from headwater channels because the narrowly incised and bedrock-dominated channels provide no potential refugia. In addition, debris flows initiated from the top (or near the top) of the channel and the entire headwater channel, including small side tributaries, were essentially affected. The colonization patterns of invertebrates significantly influence community structure after a disturbance (Mackay 1992; Vieira et al. 2004); for instance, invertebrate taxa with short generations, high dispersal abilities, or both dominate the early stage of community recovery. *Baetis*, a dominant genus in streams with recent debris flows, is a common rapid colonizer after disturbances due to its short generation period and the flight ability of adults (Mackay 1992; Vieira et al. 2004). In contrast, *G. nipponensis* would have a limited ability to disperse and colonize among streams due to its inability to fly. The complete absence of *G. nipponensis* in streams with recent debris flows is likely due to colonization limitations of individuals after population extinction by debris flows rather than to lethal environmental conditions because water flow was perennial, water temperature and chemistry were not extreme, and other taxa were present in these streams.

Invertebrates that are found only in headwater streams (headwater taxa in this study) are considered to be at a greater disadvantage for colonizing disturbed headwater streams than are those that also distribute in downstream reaches (larger-stream taxa). Because debris flows initiated

in the uppermost reaches of the channels, our headwater streams lacked an upstream source of colonists. In addition, due to the deeply incised headwater drainages in our study area, direct dispersal of headwater taxa across the ridges between streams is less probable (even with flight ability), and most dispersal would occur via the larger streams that connect the headwater channels. For headwater taxa whose dispersal is largely biased in the upstream direction, moving down to a larger stream would be a rare event (Lowe et al. 2006); this limits colonization into other headwater streams. By comparison, larger-stream taxa can more easily colonize headwaters immediately upstream. Thus, headwater taxa may be less abundant in streams with recent debris flows due to considerable limitations in the colonization process compared with larger-stream taxa.

Our results indicate that at least several decades are required for macroinvertebrate community recovery after a debris flow. The time intervals after a debris flow that separate the two groups of macroinvertebrate communities lie between 16 years (MF28 and MF31) and 38 years (MF42). Such long periods of recovery might be associated with the colonization limitations of macroinvertebrates among headwater streams as well as the changes in channel characteristics previously discussed. Although recurrence intervals of debris flows are typically relatively long (100–1000 years; Bilby et al. 2003), which enables invertebrates to recover sufficiently after the disturbances, debris flows can occur more frequently in our catchments due to a high-rainfall environment, natural instability of steep slopes, and forest management practices that may induce landslides and debris flows (Imaizumi et al. 2008). Recoveries of macroinvertebrates within a few years after debris flows have been reported in previous studies (Lamberti et al. 1991; Kiffney et al. 2004; Snyder and Johnson 2006) where there were undamaged reaches upstream.

Our study also showed that influence of debris flows are not equal among macroinvertebrate taxa, and some taxa can be positively affected by debris flows over a time scale of a few decades. An example is larger-stream taxa, which appear to expand their distribution to headwater channels as a consequence of debris flow occurrence. Headwater channels are not the main habitat of these taxa, but they can be a source of colonists when populations in downstream reaches are damaged by disturbances.

Influences of debris flows on the food web structure

Debris flows also appeared to affect the food web structure and the function of macroinvertebrates by reducing shredder mass, which was more than two orders of magnitude lower in streams of middle-aged forests than in the other streams. As a consequence, streams of middle-aged forests had lower nonpredator mass and were largely dominated by grazers. The primary food resource of the macroinvertebrate food web in the streams of middle-aged forests is likely algae, whereas in streams of recently logged and mature forests, it is likely plant litter. Low shredder mass can also result in the reduced breakdown of litter (e.g., leaves and needles) in the channel because macroinvertebrate shredders often contribute substantially to the breakdown process in headwater streams (Wallace et al. 1982; Cuffney et al. 1990; Hieber and Gessner 2002). The function of *G.*

nipponensis, which comprised most of the shredder mass in streams of recently logged and mature forests, is a key to understand litter processing in these streams. Although some species of *Gammarus* are known to have different feeding strategies and functional roles (Kelly et al. 2002), *G. nipponensis* appears to be an effective shredder in our streams because it often exhibited high densities in depositional areas and intensively colonized and shredded leaves in artificially installed bags (S. Kobayashi, unpublished data).

Despite low nonpredator mass, the predator mass in streams of middle-aged forests was not consistently low, which is different from the findings in headwater streams of Appalachia, where predator biomass was largely correlated with primary consumer biomass (Wallace et al. 1999). The predator mass may be limited by the availability of hiding areas (e.g., between or beneath stones) rather than by food in our bedrock-dominated streams. The taxa that dominated the predator mass (e.g., stoneflies and dobsonflies) had large body sizes and were often found beneath cobbles and boulders.

In summary, we examined among-stream variations in macroinvertebrate communities through year-round surveys in 10 headwater streams with different legacies of disturbances (clearcutting and debris flows). The separation of communities between the streams with and without recent debris flows suggests the importance of debris flows in structuring macroinvertebrate communities in headwater streams. Macroinvertebrate communities in streams with recent debris flows were characterized by low abundances of shredders and crawlers that favor slow-flow habitats. Availability of slow-flow habitats and retention of organic matter seem to be greatly reduced by debris flow occurrence through the removal of woody debris and destruction of in-channel structures. Finally, low abundances of headwater species in streams with recent debris flows can be partially related to their limited dispersal ability, which can extend the time for community recovery after debris flow occurrence even if environmental conditions recover.

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Appendix A

Appendix Table A1 appears on the following page.

Table A1. List of taxa used in the detrended correspondence analysis and cluster analyses and assigned functional feeding groups, life-form types, and longitudinal distribution groups.

Taxa	Functional feeding group	Life-form type	Longitudinal distribution group
Dugesia sp.	Predator	Crawler	Small stream
Gammarus nipponensis	Shredder	Crawler	Headwater
Geothelphusa dehaani	Predator	Crawler	Small stream
Paraleptophlebia sp.	Collector	Crawler	Small stream
Cincticostella spp.	Grazer	Clinger	Larger stream
Drunella cryptomeria	Grazer	Clinger	Larger stream
Ephemerella setigera	Grazer	Clinger	Larger stream
Ameletus sp.	Collector	Swimmer	Small stream
Alainites yoshinensis	Collector	Swimmer	Larger stream
Baetiella japonica	Grazer	Clinger	Larger stream
Baetis thermicus	Grazer	Swimmer	Larger stream
Baetis sp.	Grazer	Swimmer	Larger stream
Bleptus fasciatus	Grazer	Clinger	Headwater
Ecdyonurus tobiironis	Grazer	Clinger	Headwater
Epeorus spp.	Grazer	Clinger	Larger stream
Ephemera japonica	Collector	Burrower	Larger stream
Yoraperla uenoa	Grazer	Clinger	Small stream
Pseudomegarcys japonica	Predator	Clinger	Larger stream
Sopkalia yamadae	Predator	Clinger	Small stream
Nipponiella limbatella	Predator	Crawler	Small stream
Togoperla limbata	Predator	Clinger	Small stream
Taeniopterygidae	Shredder	Crawler	Small stream
Amphinemura spp.	Shredder	Crawler	Small stream
Indonemoura spp.	Shredder	Crawler	Headwater
Nemoura spp.	Shredder	Crawler	Small stream
Protonemura spp.	Shredder	Crawler	Small stream
Metrocoris histrio	Predator	Skater	Small stream
Rhyacophila bilobata	Predator	Clinger	Small stream
Rhyacophila kuramana	Predator	Clinger	Headwater
Rhyacophila nipponica	Predator	Clinger	Larger stream
Dolophilodes spp.	Filterer	Clinger	Small stream
Parapsyche sp.	Predator	Clinger	Headwater
Hydropsyche spp.	Filterer	Clinger	Larger stream
Eobrachycentrus sp.	Predator	Clinger	Small stream
Micrasema hanasensis	Grazer	Clinger	Small stream
Micrasema sp.	Grazer	Clinger	Unspecified
Lepidostoma crassicorne	Shredder	Crawler	Small stream
Moropsyche sp.	Grazer	Clinger	Headwater
Uenoa tokunagai Iwata	Grazer	Clinger	Larger stream
Platambus sawadai	Predator	Diver	Small stream
Hydrocassis lacustris	Predator	Diver	Small stream
Eubrianax sp.	Grazer	Clinger	Larger stream
Grouvellinus nitidus	Grazer	Clinger	Larger stream
Antocha spp.	Grazer	Clinger	Larger stream
Dicranota spp.	Predator	Burrower	Larger stream
Hexatoma spp.	Predator	Burrower	Larger stream
Philorus sp.	Grazer	Clinger	Larger stream
Dixa spp.	Collector	Crawler	Small stream
Simulium spp.	Filterer	Clinger	Larger stream
Orthocladiinae	Collector	Clinger	Unspecified